GEOLOGICAL SURVEY OF CANADA
PAPER 88-8

PERMIAN CONODONT BIOSTRATIGRAPHY OF THE HARPER RANCH BEDS, NEAR KAMLOOPS, SOUTH-CENTRAL BRITISH COLUMBIA

M.J. ORCHARD and P.J.L. FORSTER

1988

Energy, Mines and Resources Canada
Énergie, Mines et Ressources Canada

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Available in Canada through

authorized bookstore agents and other bookstores

or by mail from

Canadian Government Publishing Centre
Supply and Services Canada
Ottawa, Canada K1A 0S9

and from

Geological Survey of Canada offices:

601 Booth Street
Ottawa, Canada K1A 0E8

3303-33rd Street N.W.,
Calgary, Alberta T2L 2A7

100 West Pender Street,
Vancouver, B.C. V6B 1R8

A deposit copy of this publication is also available for reference in public libraries across Canada

Cat. No. M44-88/8E
ISBN 0-660-12833-0

Canada: $5.00
Other countries: $6.00

Price subject to change without notice

Critical readers

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Original manuscript submitted: 1987-11-03
Final version approved for publication: 1988-02-09

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PERMIAN CONODONT BIOSTRATIGRAPHY OF THE HARPER RANCH BEDS, NEAR KAMLOOPS, SOUTH-CENTRAL BRITISH COLUMBIA.

Abstract

In the area around the Kamloops quarry of Canada Cement Lafarge Ltd., the Permian Harper Ranch beds comprise a succession of structurally stacked, bedded carbonate. 84 new conodont collections include 21 conodont taxa and are assigned to 5 faunas and 2 subfaunas which are dated as late Wolfcampian (late Sakmarian) through late Leonardian. Some of the Harper Ranch conodonts are not known within autochthonous American sequences but are known from Japan and China, implying a western paleo-Pacific influence. Similarly, the range of some taxa, particularly Sweetognathus, *are anomalous compared with North American sequences but are similar to Asiatic records. Early Permian geographic separation from North America is favoured as an explanation, although divergent species concepts may also account for some discrepancies. The taxonomy of the stratigraphically important* Neostreptognathodus, Neogondolella *and* Sweetognathus *is reviewed. A study of fauna, conodont biofacies, and carbonate lithofacies of the Harper Ranch beds indicate a progressive increase in water depth in the study area during the Early Permian.*

Résumé

Autour de la carrière de la société Canada Cement Lafarge Ltd, à Kamloops, les couches permiennes de Harper Ranch renferment une succession de roches carbonatées stratifiées, structuralement empilées. On y retrouve 84 nouvelles collections de Conodontes qui comprennent 21 taxons de Conodontes que l'on rapporte à cinq ensembles fauniques et deux ensembles sous-fauniques, datant du Wolfcampien supérieur (Sakmarien supérieur) jusqu'à la fin du Léonardien supérieur. Certains de ces Conodontes sont absents dans des séquences autochtones américaines, mais présentes au Japon et en Chine, laissant supposer une influence de la partie ouest de l'ancien océan Pacifique. De même, la répartition de certains taxons, particulièrement les Sweetognathus, *ne correspond pas à celle observé dans des séquences d'Amérique du Nord, mais correspond plutôt à celle notée dans des séquences d'Asie. Néanmoins, on préfère l'hypothèse de la séparation de l'Asie et de l'Amérique du Nord au début du Permien, bien qu'on reconnaisse l'effet des concepts d'espèces divergentes et la possibilité d'un remaniement survenu au cours du Léonardien. On procède actuellement à la révision minutieuse de la taxinomie des* Neostreptognathodus, Neogondolella *et des* Sweettognathus *qui ont une importance stratigraphique. Une étude de l'ensemble faunique, des biofaciès des Conodontes et des lithofaciès des roches carbonatées des couches de Harper Ranch témoigne de l'augmentation progressive, au cours du Permien inférieur, de la profondeur de l'Océan dans la région à l'étude.*

INTRODUCTION

Permian conodonts from the Harper Ranch beds were first described by Orchard (1984b) who summarized the results of reconnaissance sampling of the upper terraces of the quarry of Canada Cement Lafarge Ltd., east of Kamloops in southern British Columbia (Ashcroft map area, NTS 92I). Subsequent to that report, further work was carried out within the quarry and surrounding hillside. As a result of processing about 250 kg of carbonate, many new data have been gathered and the age-range of the limestone is now known to be greater than the mid Early Permian age indicated by the original conodont collections (Orchard, 1987). Conodont control is now more consistent with the reports of earlier workers who found Wolfcampian, Leonardian and Guadalupian fossils in the limestone (Miller and Warren, 1933; Miller and Crockford, 1936; Thompson and Verville, 1950; Skinner and Wilde, 1966; Sada and Danner, 1976; Nelson and Nelson, 1985), although many of the collection sites on which these reports were based are unknown.

The purpose of this study was to determine the nature and succession of conodont faunas within the Permian part of the Harper Ranch Group. The results provide a standard against which conodont faunas from other juxtaposed Cordilleran terranes may be compared. In addition, this paper reviews taxonomic problems that have impaired intercontinental correlation (and ultimately the development of a standard Permian time scale), and presents stratigraphic and structural results.

Acknowledgements

We thank the staff of Canada Cement Lafarge Ltd. for free access to their quarry, and J. Beyers for help in the field. W.R. Danner, C. Henderson, J.W.H. Monger, and B.S. Norford kindly read earlier drafts of this paper and made useful suggestions for its improvement. P.J.L. Forster contributed to this work whilst at the University of British Columbia.

GEOLOGY

The Harper Ranch Group (Sada and Danner, 1976; Smith, 1979; Monger and McMillan, 1984) represents the Paleozoic basement of the Quesnel Terrane ("Quesnellia"), which underlies the Intermontane Belt of southern British Columbia (Fig. 1). As presently conceived, the group includes limestone, argillite, siltstone, local coarser clastics, volcaniclastics and minor chert (Monger and McMillan, 1984). Formal definition and subdivision of the group has been hampered by poor outcrop and limited age control. Conodont sampling, carried out initially in conjunction with regional mapping of the Ashcroft map area (op. cit.), has yielded conodont faunas of Late Devonian (Famennian), and Early Carboniferous (late Visean-early Namurian) age as well as the Permian faunas described herein.

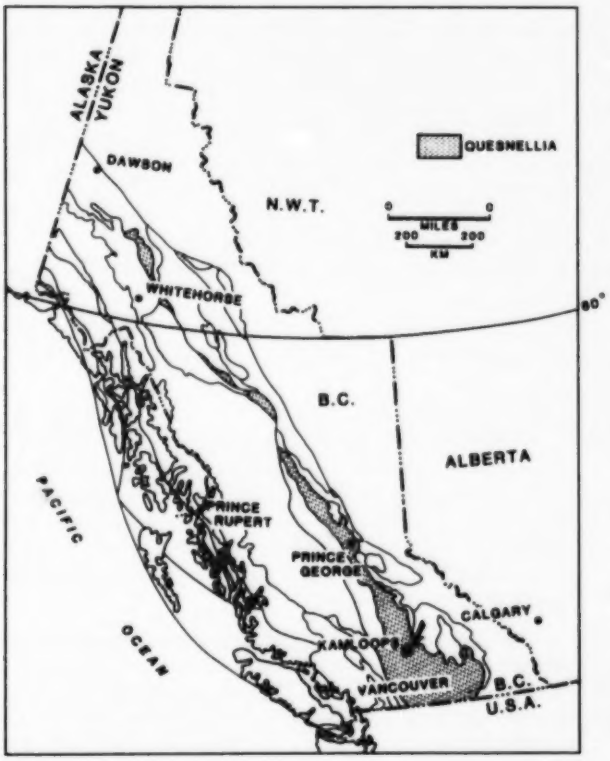

Figure 1. Location of study area with respect to Cordilleran terranes.

A Late Devonian fauna is found in a plant-bearing clastic unit known from a single locality. The relationship of this sequence with the more widespread late Mississippian siliceous limestone is unknown. Permian limestone has been reported to lie paraconformably above the Carboniferous limestone farther north in the Dome Hills (Sada and Danner, 1976, p. 217), but this contact has not been identified in the present area where undated limestone outcrops discontinuously between similar strata of proven Carboniferous and Permian age in the northwestern part of the area. Late Carboniferous strata have not been identified in the area.

The relationship with the overlying Triassic Nicola Group is also assumed to be an unconformity although the two groups are generally seen in structural contact. Most of the fossils from limestone pods within the largely volcanic Nicola Group are Late Triassic, although Middle Triassic conodonts have been recovered from inter-pillow carbonate west of the present study area.

Figure 2 shows the conodont collection sites in the area of the Kamloops quarry of the Canada Cement Lafarge Ltd., and the inferred areal distribution of the five Permian conodont faunas described below. This map, based largely on isolated conodont collections and our assessment of their relative age, shows at least two steeply dipping (50-80° SE) sequences repeated by a major fault on the west margin of the quarry. As expected from the predominant southeasterly dip, the outcrops generally young eastward but near the margin with the Triassic Nicola Group the structure is more complex. The minimum thickness of the Permian carbonates is 130m from measured sections, but calculated from figure 2, the total is perhaps 2 or 3 times that.

CONODONT FAUNAS

Orchard (1987) summarized the conodont biostratigraphy of the Harper Ranch Group and recognized five conodont faunas (Faunas 1-5) within the Permian limestones. Faunas 3 and 5 are amenable to further subdivision. Each of the faunas is described below, and their age and correlation are discussed. Numerical data are presented in Tables 1-3. Figure 3 presents a summary of the conodont range and faunas.

Fauna 1 — the Adetognathus fauna

Composition

This fauna was described by Orchard (1984b) based on 1980 sampling of a section near the top of the Kamloops quarry of Canada Cement Lafarge Ltd. (A-A' in Fig. 2). The 1980 collections consisted of the following species in order of abundance: *Adetognathus paralautus* Orchard, *Sweetognathus inornatus* Ritter, *Hindeodus* sp., *Neogondolella bisselli* (Clark and Behnken), *Diplognathodus augustus* Igo, and *Ellisonia conflexa* (Ellison). Collections made in 1984 from a lower terrace (K3-K9) duplicated this fauna in the abundance of *Adetognathus* but contained more numerous *Neogondolella* and no *Diplognathodus*. In most collections of Fauna 1, *Adetognathus* makes up at least half of the total number of elements.

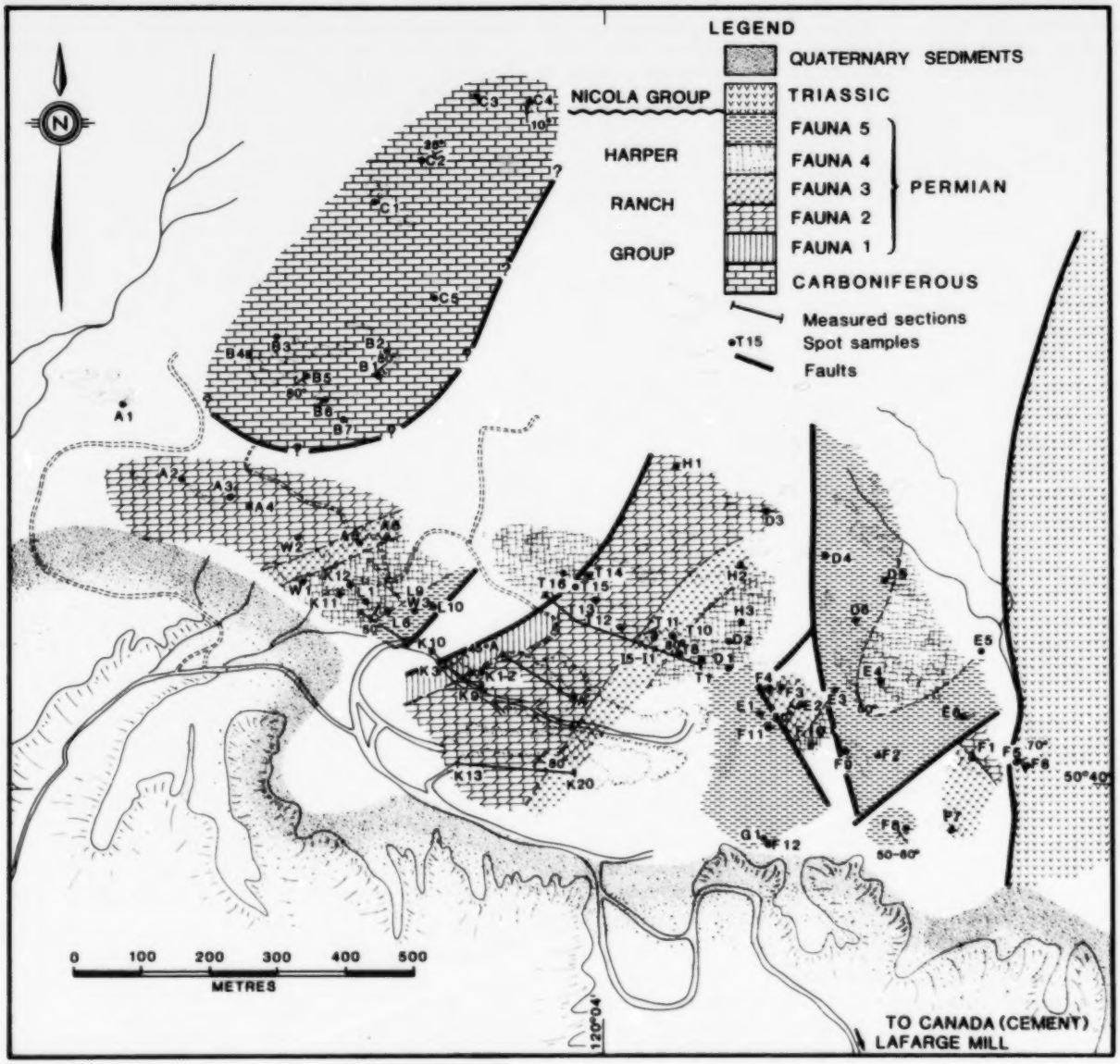

Figure 2. Geology of Harper Ranch Group in the vicinity of quarry of Canada Cement Lafarge Ltd., near Kamloops. The distribution of Conodont Faunas 1-5 are based on numbered sections and spot samples. Sample L9 = W3 = locality of Nelson and Nelson (1985). See Monger and McMillan (1984) for regional context.

Age and correlation

Fauna 1 is correlated with the late Wolfcampian of the western U.S.A. According to Ritter (1986, p. 150), the occurrence of *Sweetognathus inornatus* in Nevada, Utah, Wyoming, Texas, and Kansas, is equivalent to the Uralian late Sterlitamakian and Aktastinian Substages (Sakmarian Stage). In the Harper Ranch collections, *S. inornatus* is only identified within Fauna 1; similar forms in Faunas 2 and 3 are smaller and are regarded as early growth stages of *S. whitei*. The Kamloops occurrence of S. inornatus is therefore thought to represent the oldest part of the species' range. *S. inornatus* has not been reported from the U.S.S.R., although the first *Sweetognathus* has been reported from within the late Sakmarian (Movshovich, 1984, Table 8).

Within the Cisural and Cisdonets troughs, the cosmopolitan *Neogondolella bisselli* species first appears at the base of the Tastubian Substage of the Sakmarian

Table 1. Numerical and faunal data on Carboniferous and Permian conodont Faunas 1 and 2. Arrows under sample numbers indicate collections come from section. Abbreviations: m = miliolids, f = fusulinids, x = other foraminiferids. For other abbreviations see Figure 2.

GSC loc. no.	C-116784	C-116786	C-116787	C-116755	C-117794	C-116060	C-116054	C-116055	C-116056	C-117795	C-117796	C-117797	C-116071	C-116057	C-116058	C-116059	C-116051	C-116052	C-116064	C-116065	C-116066	C-116067	C-116068	C-116797	C-116069	C-118866	C-118865	C-118864	C-118863	C-116763	C-116759	C-117800
Sample no.	B2	B3	B4	C5	A1	K10	K4	K5	K6	A2	A3	A4	W2	K7	K8	K9	K1	K2	K14	K15	K16	K17	K18	18A	K19	T15	T14	T13	T12	H1	D3	F1
Conodonts							→		←					→		←	→								←	→			←			
Idiopriniodus sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gnathodus bilineatus	1	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lochriea commutata	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Adetognathus paralautus	-	-	-	-	-	-	141	49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diplognathodus augustus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	10	-	1	-	-	-	-	-	-	-	-	-	-	-
Ellisonia sp.	-	-	-	-	?1	?1	-	-	4	-	?1	2	-	-	-	-	2	-	4	-	1	8	-	1	2	-	-	-	-	-	-	1
Hindeodus sp.	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	3	-	1	-	-	3	1	?1	7	-	-	-	-	1	-	-
Hg. bisselli	-	-	-	-	-	-	24	1	2	-	-	-	3	-	?3	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-
Hg. n. sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Sweetognathus behnkeni	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S. inornatus	-	-	-	-	-	-	1	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S. whitei	-	-	-	-	-	-	-	-	-	3	-	?1	9	-	-	-	-	1	1	3	1	5	3	4	31	1	1	5	2	2	2	6
Total conodonts:	2	1	3	1	1	1	167	50	9	3	1	3	13	2	3	1	5	1	17	3	3	16	4	6	40	1	1	7	2	3	2	8
FAUNA NO:	CARB.				?		1			2																						?
Foraminifera:	m	-	-	m	-	-	-	-	-	f	f	-	f	-	-	-	-	-	-	-	-	f	-	-	f	-	-	-	f	f	f	f
Weight of rock dissolved (kg):	6.6	2.0	2.0	1.8	2.1	2.6	3.3	2.6	3.0	1.8	2.0	1.9	3.3	2.6	1.3	1.9	2.5	3.3	2.9	3.1	1.7	3.1	1.3	2.1	5.2	1.4	0.7	1.8	1.8	1.8	1.8	1.9

(Movshovich, 1984, Table 8) where it is associated with Carboniferous holdovers, including *Adetognathus*. In the southern Urals, the species is recorded as early as the upper Asselian (Akhmetshina et al., 1984, Fig. 2). Both these occurrences are prior to the appearance of *Sweetognathus*, as are some occurrences in western North America (Orchard, 1984b, p. 208), although not in cratonal sequences in the southern Canadian Rocky Mountains (Henderson and McGugan, 1986), Nevada (Ritter, 1987, p. 386), and Bolivia (Suarez Riglos et al., 1987).

In the U.S.S.R., both *Neogondolella bisselli* and *Adetognathus* range upward into the Aktastinian Substage of the Artinskian. Other elements of the Harper Ranch Fauna 1 appear to be equally long ranging. *Diplognathodus augustus* was originally described from the Late Sakamotozawan to Early Nabeyaman Stages in Japan: associated conodonts correlate with the Kamloops Faunas 3-4. The range of the American *D. stevensi*, regarded here as a synonym, is largely within the late Wolfcampian (Aktastinian equivalent) according to Ritter (1986), so the diplognathodid has a long range. The species of *Ellisonia* and *Hindeodus*, as presently conceived, have little stratigraphic value.

Fauna 2 — the Sweetognathus whitei fauna

Composition

This fauna is characterized by the nominate species, which developed from *S. inornatus* coincident with the disappearance of *Adetognathus* (Orchard, 1984b), the last of the "Carboniferous holdovers". Associated conodonts are the same as in Fauna 1. Both *Ellisonia* and *Hindeodus* occur regularly, whereas *Neogondolella* is sparsely represented. Diplognathodus occurs sporadically, but is occasionally common (K14). In addition, a single *S. behnkeni* is identified in one collection (W2), and a single *Neogondolella* n. sp. A occurs in a second (F1). The latter species occurs elsewhere only in Faunas 3 and 4, so the inclusion of this particular faunule (sample F1) in Fauna 2 is questioned.

Age and correlation

Fauna 2 corresponds to the widely recognized zone characterized by a co-occurrence of *Sweetognathus whitei* and *Neogondolella bisselli*. Ritter (1987, p. 397) has recently modified the scope of the *bisselli — whitei* Zone (see Orchard, 1984b, p. 208-09), redefining the base at the first appearance of *S. whitei*, and the top at the first appearance of *Neostreptognathodus pequopensis*. This overcomes the problems arising from the different ranges of the nominate species, and the broad scope of the original range zone.

As discussed by Orchard (1984b, p. 209) and Henderson and McGugan (1986, p. 224), there are discrepancies in the age attributed to the *bisselli — whitei* Zone. The nominate species occur in the basal part of the Skinner Ranch Formation, the Leonardian lectostratotype, in the Glass Mountains of west Texas (Carr and Behnken, in Cys, 1981, p. 192), and therefore the zone is, at least in part, of early Leonardian age. However, Ritter (1987, p. 397) regards the disappearance of *S. whitei*, a little above the top of the redefined *bisselli — whitei* Zone, as coinciding with the Wolfcampian — Leonardian boundary. The position of the latter

boundary with respect to the *bisselli — whitei* Zone remains uncertain (Fig. 3).

The correlation of the *S. whitei* fauna with sections in the U.S.S.R. also poses problems. The critical datum, the definite appearance of *Sweetognathus whitei*, occurs at the base of the Artinskian (Burtsevkian) (Movshovich, 1984, Table 8; contrast Bando et al., 1980, p. 15). Akhmetshina et al. (1984, p. 52, Fig. 3) record *S. whitei* even lower, within Sakmarian deposits (palynological determination) of the Caspian Depression. Formerly, the *bisselli — whitei* Zone has been recognized (Kozur, 1978) within the higher Artinskian (lower Baigendzhinian/ Sarga) where *Sweetognathus whitei* is more common, but correlation with that horizon is not necessary. Rare representatives of 'Carboniferous' holdovers overlap with *S. whitei* within both the lower Artinskian of the U.S.S.R., and in Kansas and Utah (Ritter, 1987, p. 391).

In Nevada and west Texas, *Sweetognathus behnkeni* occurs within the *bisselli — whitei* Zone (Ritter, 1986, 1987). In contrast, in Bolivia, Suarez Riglos et al. (1987) found *S. behnkeni* in younger strata associated with *N. pequopensis*. Although the ranges of *S. whitei* and *S. behnkeni* were found to be mutually exclusive in Bolivia (op. cit.), we interpret some specimens differently (see taxonomy) so the two species probably do co-occur in Bolivia. Nevertheless, *S. behnkeni* appears to have a range into the early Leonardian.

In Japan, the base of the relatively long ranging *bisselli — whitei* Assemblage Zone coincides with the appearance of *Pseudofusulina vulgaris* (Igo, 1981), and as a whole corresponds to the upper half of the *Pseudoschwagerina* Zone (Igo and Hisada, 1986, p. 518).

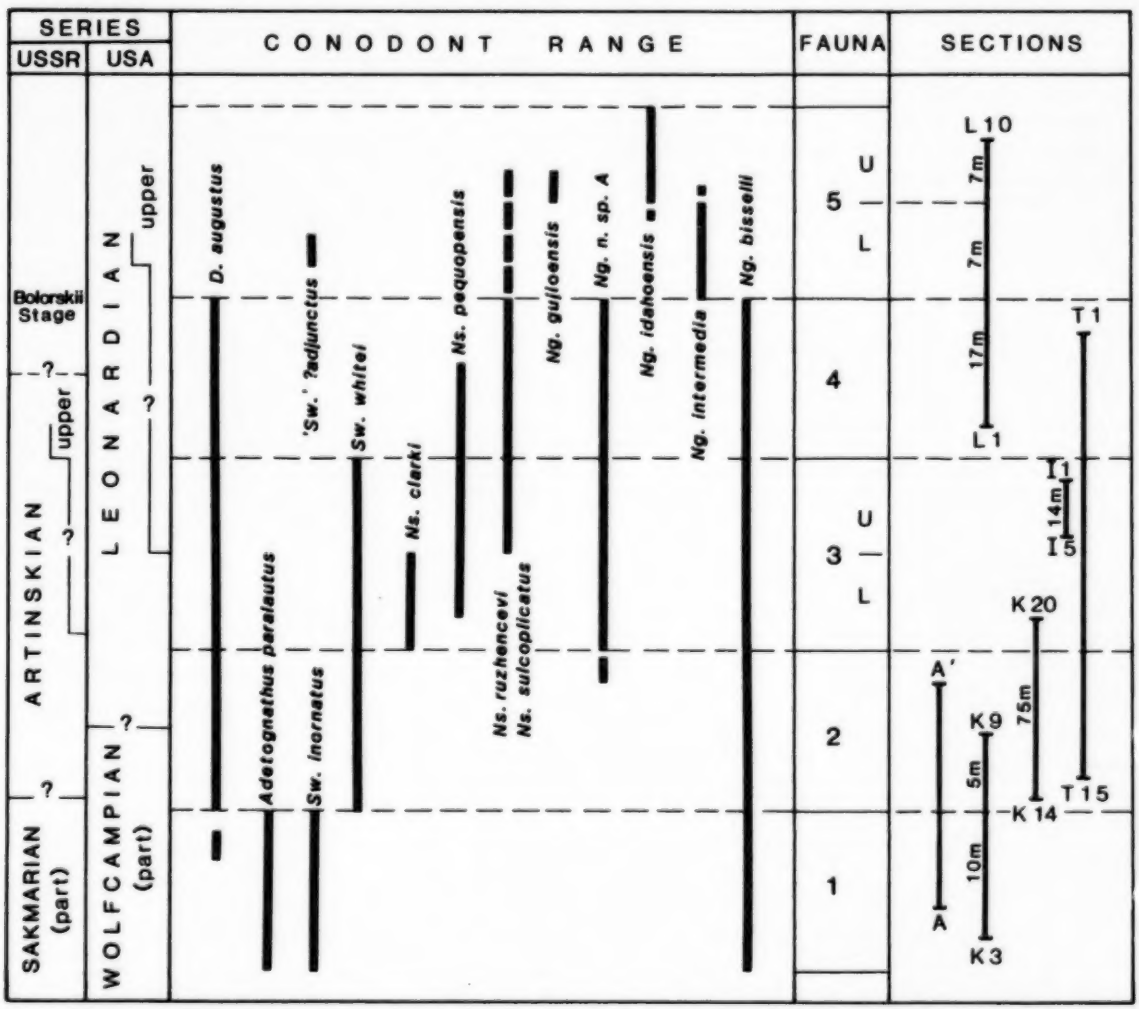

Figure 3. Harper Ranch conodont Faunas 1-5: conodont range (centre), age and correlation (left), and coverage and thickness of sections (right). Abbreviations are D. = *Diplognathodus*, Sw. = *Sweetognathus*, Ns. = *Neostreptognathodus*, Ng. = *Neogondolella*.

Elsewhere in Canada, correlatives of Fauna 2 have been described from the lower Ross Creek Formation of the Ishbel Group in southeastern British Columbia (Henderson and McGugan, 1986).

Fauna 3 — the Sweetognathus — Neostreptognathodus overlap fauna

Composition

Fauna 3 is recognized by a co-occurrence of *S. whitei* and *Neostreptognathodus* spp. As in Faunas 1 and 2, *Neogondolella bisselli* is an important constituent in this Fauna, but in addition N. n. sp. A occurs, albeit rarely. *Diplognathodus*, *Ellisonia* and *Hindeodus* species range throughout the interval.

Sweetognathus whitei co-occurs with *N. pequopensis*, or its close relative *N. clarki*, in 3 or 4 faunules. Two further collections (section T) lie above the incoming of *Neostreptognathodus* but contain only *Sweetognathus*: this raises the possibility that faunules assigned to Fauna 2 may be impoverished examples of Fauna 3. The remaining 9 faunules referred to Fauna 3 contain representatives of the *N. ruzhencevi — N. sulcoplicatus* group in addition to rare specimens of *N. pequopensis*. This distribution of *Neostreptognathodus* species forms a basis to subdivide Fauna 3 into lower and upper parts.

Age and correlation

Behnken (1975a,b) documented the overlap of *Sweetognathus whitei* with *Neostreptognathus pequopensis* in the lower part of the Pequop Formation of Nevada. Later, Kozur and Mostler (1976, p. 23-24) referred the neostreptognathodids to *N. clarki*. In Kamloops, both species of *Neostreptognathodus* are identified in the lower part of Fauna 3, which falls within the *N. pequopensis* Zone, the oldest Leonardian zone recognized by Wardlaw (in Mytton et al., 1983, p. 295) based on sections in Idaho and Nevada.

In the U.S.S.R., a combined zone of *Neostreptognathodus pequopensis — N. ruzhencevi* is recognized above the *bisselli — whitei* Zone in the upper part of the Upper Artinskian (upper Baigendzhinian — Bando et al., 1980; Sarga Horizon — Movshovich, 1984). The nominate *Neostreptognathodus* species and others, including N. clarki, appear simultaneously. The base of the *pequopensis — ruzhencevi* Zone is marked by the disappearance of *S. whitei* in the Uralian sequence (Bando et al., 1980). Hence, there is no equivalent to the Harper Ranch Fauna 3 in the Ural region.

In China, similar conodonts to those in lower Fauna 3 occur in the lower part of the Chihsia Formation in Ziyun, Guizhou (Wang and Wang, 1981, p. 228). However, Bando et al. (1980) refer the sweetognathids to *S. guizhouensis* which they regard as more highly evolved than *S. whitei* (op. cit., p. 13-14). This correlation remains uncertain.

Table 2. Numerical and faunal data on Permian conodont Faunas 3 and 4. Arrows under sample numbers indicate collections come from section. Abbreviations: f = fusulinids, x = other foraminiferids. For other abbreviations see Figure 2.

GSC loc. no.	C-117799	C-118862	C-118861	C-118860	C-116799	C-116764	C-116770	C-116769	C-116768	C-116767	C-116766	C-116773	C-116772	C-116792	C-116776
Sample no.															
Conodonts	A6	T11	T10	T9	K20	H2	I5	I4	I3	I2	I1	F4	F3	E2	F7
D. augustus	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
Ellisonia sp.	-	-	-	-	?1	-	-	1	2	-	4	6	5	7	-
Hindeodus sp.	-	-	-	1	-	-	-	1	1	-	-	-	-	7	-
Ng. bisselli	2	-	-	3	-	15	?1	4	-	?1	-	-	?1	3	?2
Ng.?intermedia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ng. n. sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Ns. clarki	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ns. pequopen.	-	-	-	-	1	?1	-	-	-	-	1	-	2	3	-
Ns. ruzhencevi	-	-	-	-	-	-	-	-	-	-	-	7	-	1	-
morph.	-	-	-	-	-	-	-	-	1	?1	-	1	-	?1	-
Ns. aff. rus.	-	-	-	-	-	-	1	-	4	1	-	9	-	2	-
Ns. sulcoplic.	-	-	-	-	-	-	1	-	6	-	-	9	?1	-	-
Ns. sp. indet.	-	-	-	-	-	-	1	-	18	1	1	28	3	8	3
Sw. whitei	10	4	1	5	12	2	2	4	2	-	?1	1	9	16	?1
Total cons:	13	5	1	9	14	18	6	10	34	4	7	61	21	53	6
FAUNA NO:	lower 3						upper 3								
Forams:	f	f	f	?f	?f	-	-	-	-	-	-	-	x	-	-
Wt. of rock dis. (kg)	1.9	2.0	1.9	1.9	2.0	1.6	2.4	2.0	2.0	2.1	2.0	1.8	1.6	2.0	1.5

GSC loc. no.	C-116070	C-116061	C-116062	C-118797	C-118798	C-118799	C-118800	C-118804	C-118867	C-118858	C-118857	C-118856	C-118855	C-118853	C-118852	C-118851	C-116765	C-116753	C-116779	C-116794
Sample no.																				
Conodonts	W1	K11	K12	L1	L2	L3	L4	L5	T16	T8	T7	T6	T5	T3	T2	T1	H3	D2	F10	E4
D. augustus	-	1	-	1	-	-	1	-	-	-	-	-	-	?1	1	-	-	-	-	1
Ellisonia sp.	3	5	2	1	1	1	4	1	-	?1	1	1	-	-	1	1	5	-	3	4
Hindeodus sp.	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	3	-	-	1
Ng. bisselli	-	4	?1	-	-	4	3	-	?2	-	-	2	-	-	?1	1	4	-	?2	4
Ng.?intermedia	-	-	-	-	-	?1	4	3	-	-	-	-	-	-	-	-	-	-	-	-
Ng. n. sp. A	-	-	-	-	-	?1	1	-	-	-	-	-	-	-	?1	-	5	?1	-	-
Ns. clarki	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ns. pequopen.	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-
Ns. ruzhencevi	2	3	5	-	4	4	7	7	-	-	-	-	-	-	-	2	5	10	25	27
morph.	-	-	1	-	?1	1	2	1	1	-	-	1	-	-	-	3	-	2	-	1
Ns. aff. rus.	7	1	1	-	8	6	9	11	1	1	1	13	1	-	-	8	4	6	3	15
Ns. sulcoplic.	1	4	-	-	4	4	12	5	-	-		5	-	-	-	3	3	6	9	5
Ns. sp. indet.	19	13	5	6	14	19	11	26	2	3	2	16	4	3	5	31	10	11	25	27
Sw. whitei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?1	-	-	-	-
Total cons:	32	31	15	8	32	41	56	54	7	5	5	38	7	4	9	50	40	36	67	85
FAUNA NO:	4																			
Forams:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Wt. of rock dis. (kg)	2.9	2.9	1.9	1.9	2.4	1.4	2.8	2.3	1.8	0.3	1.7	1.7	1.7	1.9	1.7	2.0	1.8	1.6	1.7	1.8

The upper part of Fauna 3 is recognized by the co-occurrence of both *S. whitei* and *N. pequopensis* with elements of the *ruzhencevi — sulcoplicatus* group. *N. sulcoplicatus* sensu stricto is characteristic of the upper Leonardian in the United States, so the occurrence of similar elements in Fauna 3 is therefore unexpected (see also Fauna 4). Correlation of the Harper Ranch upper Fauna 3 with the *sulcoplicatus* Zone of American authors would imply a stratigraphic break within Fauna 3, the occurrence of *Sweetognathus whitei* resulting from reworking. An intra-Leonardian unconformity is widespread in western North American cratonal sequences (Mytton et al., 1983; Henderson and McGugan, 1986), and this interpretation would provide a stratigraphic link between Quesnellia and the craton. An alternative explanation is that *N. sulcoplicatus* appears earlier in the Harper Ranch Group than in both the U.S.A. and U.S.S.R.. This explanation is supported by the absence of *Neogondolella* ex gr. *idahoensis* in Fauna 3 (and 4). Furthermore, a parallel can be drawn between the Harper Ranch Group and the Yoro Group of Japan in which *S. whitei* does co-occur with neostreptognathodids identified as *N. sulcoplicatus* (Igo, 1981, p. 20; see also Wang et al., 1987, Fig. 2, for a similar overlap in China), although this determination is difficult to confirm on the basis of published illustration. However, *N. ruzhencevi* has not been reported from Japan, and details of the Japanese succession (Igo, 1981, Fig. 13) are equivocal. Resolution of this problem rests on a thorough description of other, particularly topotype *N. sulcoplicatus* populations. *Neostreptognathodus* species concepts are discussed more fully in the taxonomic part of this paper.

A further link with the Early Permian of Japan occurs in the form of *Neogondolella* n. sp. A, previously described from the Kawanori Formation near Tokyo (Igo and Hisada, 1986), and possibly from the nearby Raidenyama Formation (Igo, 1981). The species occurs within the *bisselli — whitei* assemblage Zone of Igo (1981), which is broad in scope since it includes species of *N. idahoensis*. Igo (1981, p. 20) thought that *N.* n. sp. A and the related *N. asiatica* and *N. gujioensis* (see Fauna 5) represented a separate Early Permian neogondolellid lineage from the better known cosmopolitan *bisselli — idahoensis* line. The occurrence of the former in the Harper Ranch beds is the first record of this lineage in North America.

Fauna 4 — the Neostreptognathodus fauna

Composition

Harper Ranch faunules dominated by elements of the *N. ruzhencevi — N. sulcoplicatus* group but lacking *Sweetognathus* and the related *N. clarki* are referred to Fauna 4. As discussed under taxonomy, speciation of the neostreptognathodid group is difficult (and as presented in Table 1, probably artificial): differentiation of Harper Ranch morphotypes within the Harper Ranch Group that may be stratigraphically useful have not produced worthwhile results. The Kamloops neostreptognathodids combine features of both *N. ruzhencevi* and *N. sulcoplicatus*, and an intergrading series of morphotypes are here combined as *N.* aff. *N. ruzhencevi*.

Table 3. Numerical and faunal data on Permian conodont Fauna 5. Arrows under sample numbers indicate collections come from section. Abbreviations: f = fusulinids, x = other foraminiferids. For other abbreviations see Figure 2.

GSC loc. no.	C-116795	C-116757	C-116791	C-116780	C-116793	C-116762	C-116771	C-118805	C-118806	C-118807	C-118808	C-118809	C-118408	C-118810	C-116796	C-116760	C-116761	C-116778	C-116777	C-116756	C-116781
Sample no.	E5	D1	E1	F11	E3	D6	F2	L6	L7	L7B	L8	L9	W3	L10	E6	D4	D5	F9	F8	G1	F12
Conodonts								→						←							
Ellisonia sp.	-	-	?1	-	-	-	?1	-	-	-	-	-	-	-	-	-	-	-	-	-	?1
Hindeodus sp.	-	2	-	-	2	-	-	1	-	-	-	-	-	-	-	?1	-	-	-	-	?1
Ng. gujioensis	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Ng idahoensis	-	-	-	-	-	-	-	-	?1	-	?1	7	20	1	1	7	5	14	6	3	4
Ng. id. subsp. A	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Ng. intermedia	1	3	2	2	8	-	?2	3	1	5	2	-	-	-	-	-	-	-	-	-	-
Ng. sp. indet.	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
?Sw. adjunctus	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xaniognathus sp.	?1	5	4	4	25	6	3	5	2	5	-	4	5	-	-	?1	-	2	-	-	?1
Total conodonts:	3	11	7	6	37	6	6	9	4	10	4	11	25	1	2	9	3	16	7	3	8
FAUNA NO:	lower 5										upper 5										
Foraminifera:	-	-	x	-	-	-	-	-	-	-	f	f	f	?f	x	x	-	x	f	-	-
Weight of rock dissolved (kg):	2.0	1.1	1.7	1.7	2.0	1.8	1.7	1.0	1.4	1.9	2.5	2.8	6.1	2.3	1.8	1.9	1.7	1.9	1.8	1.6	1.8

Neostreptognathodus pequopensis occurs sporadically in Fauna 4. As in Fauna 3, both *Neogondolella bisselli* and *N.* n. sp. A occur, the latter being more common than previously, but still subordinate. Some neogondolellids resemble the younger species *N. intermedia* (e.g. L3-5), but they do not have the high blade typical of the latter species. *Diplognathodus, Ellisonia* and *Hindeodus* species range throughout the interval.

Age and correlation

In North America, *Neostreptognathodus ruzhencevi* and *N. sulcoplicatus* characterize (respectively) conodont zones immediately above the *pequopensis* Zone and near the top of the Leonardian. However, they are known to co-occur in the Grandeur Formation of the Park City Group (Wardlaw and Collinson, 1986, Table 1, p. 120), and within the lowest part of the Meade Peak Phosphatic Shale Member of the Phosphoria Formation (Behnken et al., 1986, Table 1, p. 175-6) in Idaho. The range zone of *N. sulcoplicatus* (Zone 2 of Wardlaw and Collinson, 1986, p. 127) is now correlated with the lower Roadian Stage (late Leonardian) of west Texas (Behnken et al., 1986). Earlier records of *N. sulcoplicatus* in deeper Leonardian levels (Behnken, 1975a) are now referred to *N. pnevi* (Mytton et al., 1983).

In the U.S.S.R., Kozur and Mostler (1976) established a *pequopensis* range Zone with lower and upper subzones. Later, Kozur (1978) recognized three subzones, which were elevated to zonal rank by Bando et al. (1980, p. 160). In the Cisurals, the lower subzone includes *N. pequopensis* and *N. ruzhencevi*, which appear simultaneously in the upper part of the Upper Artinskian (Movshovich, 1984) and range into the overlying Kungurian Stage. The upper subzone is named after *N. sulcoplicatus* which co-occurs with rare *N. pequopensis* and advanced *Neogondolella bisselli* (contrast the North American association with *N. idahoensis*) in the Buzterinsk Layer (upper part of Yakhtashskii Stage, lower part of Bolorskii Stage) in southeastern Pamir. Kozur and Mostler (1976, p. 16,23) regarded *N. ruzhencevi* as the precursor to *N. sulcoplicatus*, but did not record the two together. An intervening *N. pnevi* range zone was differentiated by Bando et al. (1980) in the upper part of the original lower subzone. Typical species of *N. pnevi* have not been found in Kamloops, hence there is no clear correlation with the U.S.S.R..

As discussed above, the relationship of *N. sulcoplicatus* in the Kamloops fauna to the American late Leonardian populations of *N. sulcoplicatus* sensu stricto is uncertain, partly because of the latitude given to recent determinations of the latter (see taxonomy).

Fauna 5 — the Neogondolella ex gr. idahoensis fauna

Composition

Fauna 5 is dominated by *Neogondolella* species. Two subfaunas are now recognized: the older fauna consists of forms referred to *N. intermedia*, whereas the youngest collections are characterized by typical representatives of *N. idahoensis*. Both subfaunas also contain common *Xaniognathus* sp.and rarely contain a new subspecies (*Ng. idahoensis* subspecies A).

Few other conodonts occur in Fauna 5. A single specimen referred with question to *'Sweetognathus' adjunctus* occurs in one faunule (E3) with *N. intermedia*. Incomplete specimens of *?N. gujioensis* occur in two other faunules (L8, F12). Small *Hindeodus* species, questionable *Ellisonia*, and indeterminate *Neostreptognathodus* fragments occur rarely.

Age and correlation

The range of *Neogondolella intermedia* is not well constrained at the moment. Originally described from the Kuchibora Formation and an unnamed formation in western Japan, the species occurs in early Late Sakamotozawan strata along with *bisselli — whitei* Zone conodonts (Igo, 1981). The first *N. idahoensis* appear in the topmost Sakamotozawan and the Early Nabeyaman.

Additional records of what may be *N. intermedia* are in the Trapper Creek Formation in the Cassia Mountains, Idaho (Wardlaw in Mytton et al., 1983). Associated *Neostreptognathodus* species illustrated by Wardlaw (op. cit.) include, in our terminology, the alpha morphotype of *N. ruzhencevi* and early growth stages of *N. sulcoplicatus* (identified as *N. pnevi*). The Trapper Creek Formation conodonts are therefore thought to correlate with Faunas 4-5 of the Harper Ranch Group.

In the Pamir region of the U.S.S.R., the disappearance of *Neogondolella bisselli* is coincident with the appearance of *N. idahoensis* in the Sulistyk Layer of the Bolorskii Stage, and no intermediate morphology has yet been identified. In China, forms close to both *N. intermedia* and *N. idahoensis* occur in the upper Chihsia Stage (including the *Misellina* Zone) of Guizhou. *Neogondolella slovenica*, from the late Early Permian (also the *Misellina* Zone) of NW Yugoslavia (Ramovs, 1982), is a possible synonym of *N. intermedia*.

Two fragmentary specimens close to *N. gujioensis* are recorded from upper Fauna 5. This species was originally described from the Akuda Formation in central Japan (Igo, 1981), and has a range within the upper part of long-ranging *bisselli — whitei* Assemblage Zone (Igo and Hisada, 1986). Recently, the species has also been recorded from south China (Wang and Rui, 1987). These records represents a further link between Kamloops and east Asia.

Sweetognathus adjunctus has been described from the late Leonardian uppermost Victorio Peak Formation in Texas, and the upper Pequop Formation in Nevada (Behnken, 1975a, p. 309). We are unsure whether the same species occurs in lower Fauna 5 (sample E3). Post-*whitei* sweetognathids are rare in North America, but the genus occurs through much of the Eurasian Permian.

According to Wardlaw and Collinson (1986, p. 110), *Neogondolella idahoensis* (sensu lato) ranges through the

middle Leonardian and up to about the middle of the late Leonardian where it disappears at the same time as *Neostreptognathodus sulcoplicatus*. Neostreptognathodids were therefore extant during deposition of the youngest Harper Ranch beds, as confirmed by their very rare occurrence in Fauna 5.

In the U.S.A., the topmost Leonardian is characterized by the youngest species of *Neostreptognathodus, N. newelli* and the descendant of *Neogondolella idahoensis, N. serrata* (Wardlaw and Collinson, 1986). The faunal changeover in the neogondolellid stock is widespread and well dated, occurring within the lower third of the Road Canyon Formation of west Texas (op. cit., p. 127). This represents a minimum age for Fauna 5.

CONODONT BIOFACIES — DEPOSITIONAL ENVIRONMENTS

Environmental controls on the distribution of Permian conodonts were first noted by Clark and Behnken (1971, p. 426). More recently, Ritter (1986) and Wardlaw and Collinson (1984) have presented ecological models for conodont distribution in the lower and upper parts of the Lower Permian.

Harper Ranch carbonates containing *Adetognathus* dominated Fauna 1 may indicate deposition under relatively restricted marine conditions since, in common with other cavusgnathoids, *Adetognathus* probably preferred a shallow water, and possibly a high energy habitat (Chamberlain and Clark, 1973; Heckel and Baesemann, 1975; Merrill and von Bitter, 1976; Larson and Clark, 1979). The associated *Ellisonia* may also have preferred, or tolerated, similar conditions (von Bitter and Merrill, 1983). The limestones containing Fauna 1 are crinoidal wackestones and packstones that occasionally contain brachiopods, algae and bryozoans. They are similar to underlying Carboniferous limestones, but the latter also contain articulated crinoid stems up to 2.5cm in diameter, isolated corals, and miliolid foraminiferids (m in Table 1); both limestones are generally darker than those containing Faunas 2-4. An undetermined thickness of brachiopod packstone appears to be stratigraphically higher than the conodont bearing Carboniferous limestones, and lower than the Fauna 1 limestones. These shell beds (samples C2,B5-7) did not produce conodonts and appear to represent a relatively specialized environment; they are tentatively included in the Carboniferous. Fauna 1 may date from an initial transgressive pulse that produced a favourable marine environment for conodonts early in the Permian.

Subsequent to the disappearance of the cavusgnathoids during the Early Permian (end of Fauna 1 in Kamloops), new biofacies distributions were established. Ritter (1987) has discussed these for the "post-crisis" *Sweetognathus whitei — Neogondolella bisselli* Zone in the central and western United States. Ritter (op. cit.) recognized five biofacies, several of which are known only from nearshore environments in Kansas and Texas. More open marine environments (Biofacies I) occur in Nevada where *Neogondolella bisselli* and *Sweetognathus behnkeni* are common, whereas the two species are much less common or absent in the more shelfward lithofacies of Utah and Kansas (Biofacies IIA).

Elements of both Biofacies I and IIA occur in Harper Ranch Fauna 2, but the virtual absence of *S. behnkeni* in Kamloops suggests that the depositional environment was not as deep as Biofacies I of Ritter (1987). However, the presence of *N. bisselli* suggests that there were open marine conditions within the area during Fauna 2 time. Other elements of the fauna appear to have had a broad environmental tolerance, although local abundance of *Diplognathodus* (e.g. K14) may reflect a particular environmental niche.

Lithologically, Fauna 2 limestone is a crinoidal packstone containing occasional fusulinids, algae, bryozoans, brachiopods, and?sponge spicules. As in the Carboniferous limestone, large articulated crinoid stems occur occasionally. In general, Fauna 2 limestones seem to have high percentages of framework grains and low percentages of matrix; 9/28 samples of Fauna 2 limestone contain fusulinids. We have concluded from the conodont biofacies, lithology, and the common occurrence of fusulinids, that Fauna 2 limestones represent deposition under warm and shallow, offshore marine conditions, slightly higher in energy than conditions prevailing during deposition of Fauna 4 limestones (see below).

Wardlaw and Collinson (1984, 1986) recognized five conodont biofacies (and a nearest to shore zone that lacked conodonts) in the late Early Permian sequences of the Phosphoria Basin. A nearshore biofacies was represented by *Hindeodus* alone, followed seaward by: a nearshore to intermediate biofacies containing *Neostreptognathodus* and others; a transition biofacies including, in addition to the above, *Neogondolella* or *Xaniognathus;* and an offshore biofacies dominated by the last two genera. A farthest from shore subfacies was characterized by *Neogondolella* and/ or *Xaniognathus*, and the general exclusion of others.

The diverse faunules of Harper Ranch Fauna 3 appear to represent an intermediate to transition biofacies in the sense of Wardlaw and Collinson (1984). *Neogondolella* is generally subordinate to the shallow water 'gnathodid' conodonts (the exception is sample H2) but its regular occurrence implies an offshore, deeper water influence. Furthermore, the presence of both cosmopolitan (*N. bisselli*) and asiatic (*N.* n. sp. A) species indicates the influence of a western paleo-Pacific province, no evidence of which is known in autochthonous North American sequences. Similarly, the persistence of *S. whitei* in the Harper Ranch beds long after the disappearance of the genus in autochthonous America provides further linkage with Asiatic sequences. Fauna 3 is presumed to have lived in a similar environment to Fauna 2 since many of the species are common to both faunas, and the limestones are lithologically very similar.

Fauna 4 biofacies is also similar to that of Faunas 2 and 3, although the disappearance of *Sweetognathus* may have

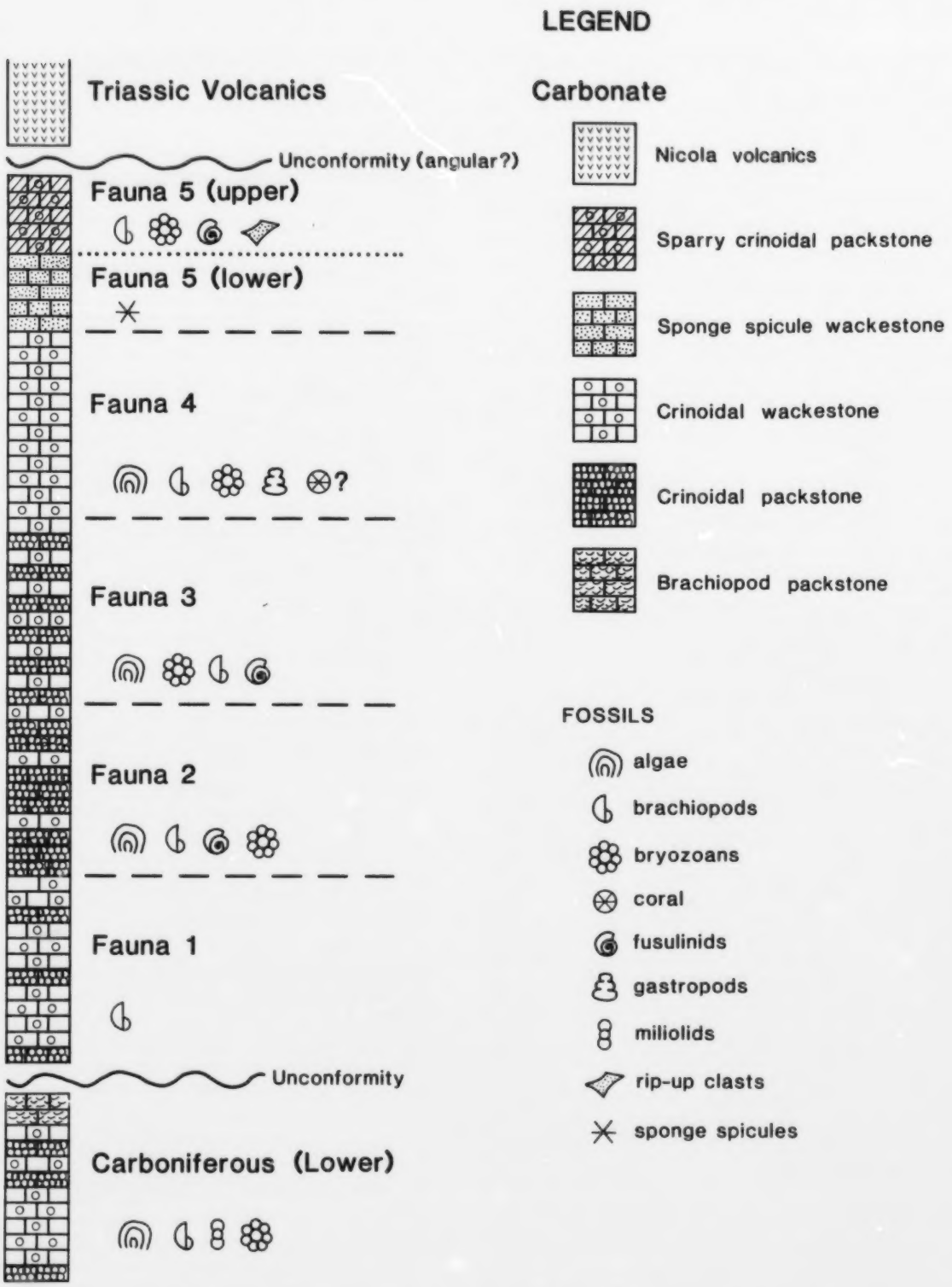

Figure 4. Idealized stratigraphic section of the Harper Ranch Permian showing lithological and faunal characteristics of carbonates bearing Conodont Faunas 1 — 5.

ecological significance because the genus (or a homeomorph) is known in younger Permian rocks, especially in parts of Eurasia. Fauna 4 limestones are crinoidal wackestones and rare packstone with brachiopods, algae, bryozoans, gastropods, and rare corals. In contrast to those containing Fauna 2, they contain more matrix and they do not contain fusulinids: this presumably reflects lower energy, and perhaps deeper and cooler conditions.

The change from neostreptognathodid dominated faunules of Fauna 4 to neogondolellid dominated faunules of Fauna 5 is sudden in section L (Fig. 2) where resistant, pale weathering, rather massive limestones are overlain by recessive, dark, thin bedded carbonates. *Neogondolella* and *Xaniognathus* completely dominate the faunules, in which all other elements are rare or absent; this corresponds to the most offshore biofacies of Wardlaw and Collinson (1984). As in Faunas 2-4, the presence of an Asiatic neogondolellid lineage is noted, in this case rare *N. gujioensis*. The cosmopolitan *N. intermedia* and *N. idahoensis* are far more common, however, and the replacement of one of the former species by the latter midway through Fauna 5 is a useful datum.

Lithologically distinct limestones characterize the lower and upper parts of Fauna 5. The lower limestones comprise dark grey, homogeneous, sponge spicule biomicrites, whereas upper Fauna 5 limestones are usually poorly sorted, richly fossiliferous crinoidal biosparites in which large brachiopods, small fusulinids, and bryozoans also occur; corals and trilobites have been reported by Nelson and Nelson (1985) from these levels. Some samples of upper Fauna 5 limestone also contain intraclasts of the underlying sponge spicule biomicrite.

SYNTHESIS

In the Kamloops area of southern British Columbia, the Harper Ranch Group includes rocks as old as Late Devonian (Famennian), but late Visean — early Namurian carbonates are the most widespread (Orchard, 1987). No Pennsylvanian conodonts have yet been found in the region so the later Carboniferous history is uncertain. On the north side of the Thompson River, in the area of the quarry of Canada Lafarge Cement Company, limestones apparently overlying proven late Mississippian strata and underlying proven Permian carbonates are devoid of conodonts and their age is undetermined. Elsewhere in the area, Danner (1976) has described a paraconformity between Carboniferous and Permian limestones, which suggests there was an intervening non-depositional event, at least locally.

Early Permian sedimentation began no later than the late Wolfcampian (Fauna 1). The limestones represent deposition in shallow water and contain a conodont fauna rich in *Adetognathus*, implying somewhat restricted marine conditions. No fusulinids were found in these carbonates, although Sada and Danner (1976) reported *Pseudoschwagerina* from the area, which would be about this age. The late Wolfcampian may have been a transgressive event that re-established carbonate bank deposition within the Harper Ranch beds.

At about the Wolfcampian — Leonardian boundary (Fauna 2), the cosmopolitan *bisselli — whitei* fauna was dominant in the Harper Ranch beds. At this time, both the carbonates and the conodont biofacies appear to represent a more open marine environment and the common occurrence of fusulinids (chiefly *Parafusulina*) implies warm, nutrient rich, shallow water. These conditions persisted through the early Leonardian (lower Fauna 3) but by the time *Neostreptognathodus* became important (upper Fauna 3), and then dominant (Fauna 4), the environment had become inhospitable to fusulinids. This situation has parallels in the Phosphoria Basin where fusulinids are absent, possibly due to cool upwelling waters (Wardlaw and Collinson, 1986, p. 129). There may have been a period of reworking between (lower) Fauna 3 and Fauna 4, producing the 'mixed' fauna of upper Fauna 3 although we prefer the alternate explanation of extended range. The carbonates of Fauna 4 are thought to have developed under moderate energy conditions in an offshore, slightly deeper water setting more conducive to the accumulation of carbonate mud.

Although Faunas 2?,3 and 4 contain elements of the offshore *Neogondolella* biofacies, these are always subordinate to the relatively shallow water 'gnathodid' group. Two *Neogondolella* lineages are represented, one being cosmopolitan in distribution, the other having previously been described only from Japan. Although the latter is rare, its occurrence suggests that there was a West Pacific influence during deposition of the Harper Ranch Group; this might also account for the anomalies in conodont range when compared with other North American sequences.

The advent of late Leonardian (Fauna 5) sedimentation marks a dramatic environmental change in the study area, which might be interpreted as the continuation of a deepening trend. *Neostreptognathodus* virtually disappeared and the offshore *Neogondolella — Xaniognathus* biofacies prevailed for the duration of proven Permian deposition in the Harper Ranch Group. The depositional environment of lower Fauna 5 was one of low energy in a relatively deep water setting in which, apart from conodonts, calcareous sponges were the only widespread fauna. Carbonates containing upper Fauna 5 are, in contrast, richly fossiliferous. One fossil collection described by Nelson and Nelson (1985) includes Tethyan waagenophyllid corals and further demonstrates a West Pacific influence for the Harper Ranch Group (*see* also Miller and Wright, 1987). These bioclastic limestones may have originated in a shallower water environment and been transported downslope as debris flows that eroded and incorporated the underlying sediments as intraclasts; there is, however, no obvious admixture of conodont biofacies.

CONCLUSIONS

1. The Permian Harper Ranch beds comprise several hundred metres of bedded carbonate that are structurally stacked and repeated in the area around the Kamloops quarry of Canada Cement Lafarge Ltd.

2. The Permian Harper Ranch beds are late Wolfcampian (late Sakmarian) through late Leonardian based on 84 new conodont collections assigned to 5 Faunas and 2 subfaunas. There is as yet no conclusive conodont evidence for Upper Permian limestones, although this is not ruled out.

3. The range of some conodonts differ compared with those of autochthonous American sequences. This may be due to: (i) Early Permian geographic separation, (ii) to a period of reworking between (lower) Fauna 3 and Fauna 4, (iii) differing species concepts. Whereas (iii) is a factor, we favour (i) as a partial explanation. We have not observed any sedimentological evidence for (ii).

4. Fauna, conodont biofacies, and carbonate lithofacies indicate a progressive deepening through much of the interval studied. During this time, the strata accumulated as a subsiding carbonate bank onto which there was little or no terrigenous or volcaniclastic input.

5. Some of the Harper Ranch conodonts are not known within autochthonous American sequences but are known from Japan and China, implying a western paleo- Pacific influence.

SYSTEMATIC TAXONOMY

Species are described below in alphabetical order. All are platform species: no multielement, suprageneric classification has been attempted. The diagnoses for most species are revised from the original.

Adetognathus paralautus Orchard 1984

Plate 1, figs. 1-5

?p. 1973 *Adetognathus lautus* Gunnell — Baesemann, p. 697, pl. 2, figs. 31,34,?29,?30.
1984 *Adetognathus paralautus* sp. nov. — Orchard (b), p. 210, pl. 23.1, figs. 15,16,20-25 (with synonymy).

Remarks:
Orchard (1984b) introduced this species for adetognathids that differed from similar species in possessing essentially identical left and right bladed elements, neither of which has a large cusp near the platform — blade junction. The holotype is reillustrated here in upper and lateral views.

Diplognathodus augustus Igo 1981

Plate 1, figs. 12, 16-18

1981 *Diplognathodus augustus* n. sp. — Igo, p.30, pl.8, figs. 1-8.
?p. 1982 *Diplognathodus stevensi* n. sp. — Clark and Carr, p.132, pl.1, figs. 9-11, 13-15.
1984 *Diplognathodus* sp. A — Orchard (b), p. 210, pl. 3.1, figs. 7,9.
1986 *Diplognathodus stevensi* Clark and Carr — Ritter, p.147, pl.3, figs. 3,5.
? 1987 *Diplognathodus oertlii* Kozur — van den Boogaard, p.22-23, fig. 6C,D.

Diagnosis:
A small species with a short blade bearing a tall anterior denticle, a partially to completely fused carina with a steep posterior edge, and an anteriorly broad, asymmetrically expanded cup that bears a concentric ridge near the perimeter.

Remarks:
As discussed by Orchard (1984b), observed differences in Early Permian *Diplognathodus* species has not been put in the context of specific variation: both blade and carina denticulation, and posterior profile vary in a non prescribed way. Ritter (1986) expanded the definition of *D. stevensi* to include the specimens reported by Orchard (1984b), but the precise scope of the former species remains unclear (*see* also von Bitter and Merrill, 1985). New material from Kamloops includes other variants that lie outside the new definition: elements with the highest blade denticle at the anterior end (Plate 1, fig. 17), and up to 7 blade denticles (Plate 1, fig. 18). However, after further comparison with *D. augustus* Igo 1981, we conclude that the Kamloops specimens lie within the concept of that species too. *D. augustus* was published on 15 December 1981, whereas *D. stevensi* was published on 25 January 1982, so the former is the senior species.

Igo and Hisada (1986) referred Japanese diplognathodids (including *D. oertlii* sensu Igo 1981) with a sloping posterior profile to Diplognathodus sp. A. However, D. sp. A of Orchard (1984b) has an abrupt posterior margin and is here included in *D. augustus*.

D. oertlii Kozur 1975 appears to be very similar, if not identical, to the present species, but it does not clearly have the ridge near the edge of the basal cup. Should it be shown to have this feature, the proper name for the present species would be *D. oertlii*.

Neogondolella bisselli (Clark and Behnken 1971)

Plate 3, figs. 1-3,7-9,?14

v. 1971 *Gondolella bisselli* n. sp. — Clark and Behnken, p. 429, pl. 1, figs. 12-14.
1978 *Neogondolella bisselli* (Clark and Behnken) — Kozur, pl.2, fig. 16; pl. 3, Figs. 6,7,10.
1981 *Neogondolella bisselli* (Clark and Behnken) — Wang and Wang, p. 229, pl. 2, figs. 16,17.
p. 1981 *Neogondolella bisselli* (Clark and Behnken) — Igo, p. 37, pl. 1, fig. 18.
1983 *Neogondolella bisselli* (Clark and Behnken) — Wardlaw *in* Mytton et al., p. 299, fig. 12/26.
1984 *Neogondolella bisselli* (Clark and Behnken) — Orchard (a), pl. 22.1, figs. 14,16,17.
1984 *Neogondolella bisselli* (Clark and Behnken) — Orchard (b), p. 213, pl. 23.1, figs. 11,17,?10.
1986 *Neogondolella bisselli* (Clark and Behnken) — Henderson and McGugan, p. 232, fig. 7/9,10-12.
1986 *Neogondolella bisselli* (Clark and Behnken) — Ritter, p. 154, pl. 1, fig. 1 (with additional synonymy through 1984).

1987 *Neogondolella bisselli* (Clark and Behnken) — van den Boogaard, p. 25, fig. 7A-F.

Diagnosis:

A *Neogondolella* species with a lachrymiform platform outline, low carina denticles, and shallow adcarinal furrows. The posterior platform margin and the basal loop are rounded.

Remarks:
As noted by Orchard (1984b), the holotype of this species has discrete anterior and posterior denticles that do not rise off the platform. This morphological feature is regarded as of primary importance in the recognition of *N. bisselli*. Usually, the posterior margin is rounded, but may be more quadrate in mature growth stages. Igo (1981, pl. 1, Figs. 10,19) referred specimens with high blades to this species but we regard these as more advanced than *N. bisselli*. Similarly, Igo and Hisada (1986) referred specimens illustrated by Orchard (1984a,b) to *N. idahoensis* in spite of the fact that they have low anterior blades: we retain these specimens in *N. bisselli*.

A few specimens from Kamloops (e.g. Plate 3, Fig. 2) have a slightly expanded cusp, a very narrow posterior brim, and platform margins that angle inward fairly sharply anteriorly. These features are characteristic of two younger species, *N. intermedia* and *N. phosphoriensis*, both of which have high anterior denticles. Several other specimens (e.g. Plate 3, figs. 7-9) also appear more advanced in that the posterior margin and basal loop are more quadrate in outline. The specimens are retained in the present species because the entire blade is low.

Neogondolella gujioensis Igo 1981

Plate 2, figs. 23,24

1981 *Neogondolella gujioensis* n. sp. — Igo, p. 37-38, pl. 3, figs. 1-19; pl. 4, figs. 1-6.
1986 *Neogondolella gujioensis* — Igo and Hisada, p. 521, pl. 97, figs. 1-9.

Diagnosis:
A species of *Neogondolella* with a broad, marginally upturned, elongate-oval platform, shallow adcarinal furrows, a relatively high carina-blade, and a small, generally terminal cusp.

Remarks:
Igo (1981) erected this species for neogondolellids that were similar to *N. bisselli* but differed in possessing relatively broad platforms. Igo and Hisada (1986, p. 522) emphasized the terminal nature of the cusp in *N. gujioensis*, thereby distinguishing it from *N.* sp. A *see N.* n. sp. A) in which a posterior brim is well developed. However, the holotype of *N. gujioensis* does have a small posterior brim even though other specimens referred to the latter species by Igo (1981) and Igo and Hisada (1986) do not.

Two specimens from Kamloops, neither of which is complete, are referred to this species. Both have a small brim, and a carina-blade that is more laterally compressed, more fused and higher than that of both *Neogondolella bisselli* and *N.* n. sp. A. One specimen also has a straight posterior margin.

Neogondolella idahoensis
(Youngquist, Hawley and Miller 1951)

Plate 3, figs. 13? 17, 22-24.

1951 *Gondolella idahoensis* n. sp. — Youngquist, Hawley and Miller, p. 361, pl. 54, figs. 1-3,14,15.
1981 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) — Igo, p. 38, pl. 1, figs. 11-13,15,16.
1986 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) -Wardlaw and Collinson, fig. 17/11,12.
1986 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) -Behnken et al., p. 179,181, fig. 4/12,13?,14-16,18 (with synonymy through 1984).
1986 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) -Ritter, p. 154-5, pl. 1, fig. 2.

Diagnosis:
A *Neogondolella* in which the platform and basal loop are flattened on the posterior edge. The platform is broadest at the posterior end, and tapers to the anterior where there is a high anterior blade; it has deep and narrow adcarinal grooves. The cusp is high, erect, and commonly terminal.

Remarks:
The Kamloops material includes some typical representatives of this species. Juvenile specimens have rounded postero-lateral corners, and a cusp and basal cavity that protrudes well beyond the posterior margin of the platform. They also have a lower blade on which pointed denticles are distinctively inclined posteriorly (e.g. *see* Igo, 1981, pl. 1, figs. 13-16). With growth, the cusp becomes submerged into the platform, the posterior nodes usually coalesce to form a nodulose ridge on the posterior 1/3 to 1/2 of the platform, and the anterior blade rises well above the platform. Fusion of the penultimate posterior denticle, cited as diagnostic by Behnken et al. (1986), is not very common in our material although it is seen in a few specimens.

During early growth, the platform is slightly wider towards the middle, but the posterior margin of the platform becomes distinctively squared off during later growth. In late growth stages, continued postero-lateral growth may produce a constriction of the platform margins just anterior to the cusp, and the medial platform may appear to broaden slightly about the middle (e.g. Plate 3, fig. 22; also Igo 1981, pl. 1, figs. 11,12), partly as a result of flattening in that area. In some large specimens of *N. idahoensis*, the carina may bifurcate (symmetrically or asymmetrically) at the posterior end of the platform. In very large specimens, a posterior brim might develop.

N. idahoensis differs from *N. bisselli* in anterior blade height and shape of the posterior loop. Posterior platform

shape is less reliable since late growth stages of *N. bisselli* may develop a more quadrate posterior outline (e.g. Orchard 1984a, pl. 22.1, figs. 16,17).

N. idahoensis and *N. phosphoriensis* are morphologically very similar. The two species differ in that the latter has a platform that is consistently broadest at midlength, lacks the large erect cusp and the adjacent fused denticle, has a small brim posterior to the cusp in most large specimens, has rounded postero-lateral platform margins, and has a basal loop that is commonly round and much smaller than that of *N. idahoensis* (Behnken et al., 1986, p. 179,181).

Neogondolella idahoensis subsp. nov. A

Plate 3, figs. 18-20.

?p. 1986 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) — Igo and Hisada, pl. 96, fig. 9 (only).

Remarks:
This unique specimen has an asymmetric, obliquely truncated posterior margin and a significantly lower length to width ratio than typical N. idahoensis; it also lacks the diagnostic large cusp. The blade, carina, and lower surface morphology are the same as those of *N. idahoensis*.

Neogondolella intermedia Igo 1981

Plate 3, figs. 10,11,12,15,16,21

1981 *Neogondolella intermedia* n. sp. — Igo, p. 38-39, pl. 4, figs. 7-11.
? 1982 *Neogondolella slovenica* n. sp. — Ramovs, p. 416-422, pl. 2, figs. 1-5; pl. 3, figs. 1-3.
1983 *Neogondolella idahoensis* (Youngquist, Hawley and Miller) -Wardlaw, *in* Mytton et al., p. 299, fig. 12/?6,7,8,?9.

Diagnosis:
A species of *Neogondolella* with a narrow platform that is moderately tapered anteriorly, has subparallel margins medially, and is symmetrically to asymmetrically rounded posteriorly. A low terminal cusp is present in intermediate growth stages, and later a brim may develop. The basal loop is rounded, the adcarinal furrows are deep and well defined, and the anterior blade is high.

Remarks:
The Kamloops specimens referred to this species occupy an intermediate morphological and stratigraphic position between *N. bisselli* and *N. idahoensis*. In contrast to the former, *N. intermedia* has a high anterior blade, posteriorly inclined denticles, and pronounced adcarinal furrows. In constrast to *N. idahoensis*, the posterior platform and loop are more rounded and the cusp is less prominent. Late growth stages of both *N. intermedia* and *N. idahoensis* display atypical, often asymmetric posterior morphology arising from bifurcation of the carina, and variable brim development.

N. slovenica Ramovs was based on very small specimens that have the widest part of the platform at, or just anterior to the middle, and a fairly pronounced taper towards the anterior end. These specimens, regarded as mature by Ramovs (1982), resemble the early growth stage illustrated herein (Plate 3, figs. 15,16).

The Late Permian *Neogondolella phosphoriensis* (Youngquist, Hawley and Miller) has a broader platform medially, a more pronounced anterior taper, and a posterior carina that has more coalescing nodes than in *N. intermedia*.

Neogondolella n. sp. A

Plate 3, figs. 4-6.

? 1975 ? *Neogondolella bisselli* (Clark and Behnken) — Malkowski and Szaniawski, p. 82, pl. 1, figs. 1a-c.
1986 *Neogondolella* sp. A — Igo and Hisada, p. 522, pl. 96, fig. 12.

Diagnosis:
A species of *Neogondolella* with a broad, elongate-oval platform with a roundly pointed posterior end, shallow adcarinal furrows, a small cusp, and a distinct posterior brim.

Remarks:
This species has a posterior brim that is well developed, unlike *N. gujioensis* (q.v.), in which the cusp is generally terminal. The Kamloops specimens have a wide, fairly flat platform on which there are 12-15 carina nodes that may be compressed posteriorly and slightly fused; the cusp is not significantly larger than other nodes. The anterior blade denticles are low. The posterior brim is upturned in some specimens.

This species is not named at present because our material is fragmentary. The specimen illustrated by Malkowski and Szaniawski (1975) also has a distinctive posterior brim but has fewer, more widely spaced denticles.

Neostreptognathodus clarki Kozur 1976

Plate 2, figs. 7?,8

1976 *Neostreptognathodus clarki* n. sp. — Kozur and Mostler, p. 12-13, pl. 2, fig. 8.
? 1976 *Neostreptognathodus transitus* n. sp. — Kozur and Mostler, p. 16, pl. 2, figs. 11,12.
1979 *Neostreptognathodus pequopensis* Behnken — Szaniawski and Malkowski, pl. 8, fig. 4.
p. 1979 *Neostreptognathodus svalbardensis* sp. n. — Szaniawski and Malkowski, p. 250-51, pl. 7, figs. 4,5 (only).
?p. 1981 *Neostreptognathodus pequopensis* Behnken — Igo, p.41, pl. 5, fig. 9 (only?).
1987 *Sweetognathus whitei (Rhodes) — Suarez Riglos et al., pl. 19.2, fig. 8.*

Diagnosis:
A *Neostreptognathodus* species with a platform ornamented by two rows of nodes that are partly separated by a medial

furrow, and partly connected by transverse ridges, usually in the posterior part.

Remarks:
According to Kozur and Mostler (1976), *N. clarki* is transitional between *Sweetognathus whitei* and *Neostreptognathodus pequopensis* (q.v.) In common with the former, several pairs of nodes on the posterior platform are joined by transverse ridges, whereas most of the medial and anterior nodes are separated, as in *Neostreptognathodus*. This morphology is common to *N. clarki* and a second species, *N. transitus*. These two species, both of which were described from the Upper Artinskian (Baigendzhinian) of the Aktasty River, in the Aktyubinskian Cisural Region of the U.S.S.R., differ principally in size, the holotype of *N. clarki* being significantly smaller than that of *N. transitus*. One cited difference between the two species is that there are joined anterior nodes in *N. transitus*, but these may occur also in *N. clarki* (Kozur and Mostler, 1976, p. 13). The basis for separating the two species is therefore questioned.

Most of the immature specimens of *N. svalbardensis* illustrated by Szaniawski and Malkowski (1979, pl. 6) have a platform outline similar to that of *N. pequopensis*, but the round nodes are orientated obliquely rather than upright. This morphology is regarded as that of a valid species, but other specimens referred to *N. svalbardensis*, including the holotype, have partly connected nodes and have been referred to *N. transitus* by Bando et al. (1980). We concur with the latter authors that accessory pustules on the basal cup are not specifically definitive.

N. toriyamai Igo 1981 from the Lower Permian of Japan is an additional species that shares a morphology intermediate between *Sweetognathus* and *Neostreptognathodus*: it differs in having a broader, biconvex platform.

Neostreptognathodus pequopensis Behnken 1975

Plate 2, figs. 1-6

p. 1975 *Neostreptognathodus pequopensis* n. sp. — Behnken, p. 310, pl. 1, figs. 21,22,25 (only).
p. 1979 *Neostreptognathodus svalbardensis* n. sp. — Szaniaski and Malkowski, p. 250-51, pl. 6, fig. 1.
1979 *Neostreptognathodus pequopensis* Behnken — Movshovisch et al., pl. 2, figs. 7a,b.
1981 *Neostreptognathodus pequopensis* Behnken — Wang and Wang, p. 231, pl. 1/ 13,19.
? 1983 *Neostreptognathodus pequopensis* Behnken — Wardlaw (*in* Mytton et al.), p. 299, fig. 12:1 (with synonymy through 1979).
? 1986 *Neostreptognathodus pequopensis* Behnken — Henderson and McGugan, p. 232, fig. 8/ 1-3.
1987 *Neostreptognathodus pequopensis* Behnken — Suarez Riglos et al., pl. 19.3, figs. 6-11.

Diagnosis:
A *Neostreptognathodus* species characterized by a platform bearing two rows of upright, round and discrete nodes.

Remarks:
Although earliest growth stages of this species were stated to have a single row of undivided nodes (Behnken, 1975a, p. 310), this has been disputed by both Szaniawski and Malkowski (1979, p. 250), and Bando et al. (1980, p. 8); we find no evidence of this morphology either. Most illustrated specimens of *N. pequopensis*, including the holotype, are relatively small specimens in which all but the posteriormost pair of nodes are separated. It is not clear how later growth stages may differ. Igo (1981, p. 41) noted that "gerontic" growth stages may have coalescing nodes and a central carina, particularly on the posterior platform, a description that corresponds to *N. clarki* (q.v.). In contrast, Suarez Riglos et al. (1987) illustrated relatively large specimens that retain discrete denticles throughout. Large specimens from Kamloops with anterior platform characteristics of *N. pequopensis* are rare, but these specimens do show greater fusion of the posterior pairs of nodes and are referred to *N. clarki* (q.v.).

Early growth stages of *N. pequopensis* may display unequal development of parapet nodes (Plate 2, fig. 1). We hypothesize that this arises from fusion of the longitudinal ridge seen in S. whitei to one lateral carina; lateral migration of this ridge is seen in one sweetognathid (Plate 1, figs. 15,20). This asymmetry can also be seen in the specimens illustrated by Movshovich et al. (1979, pl. 2, fig. 7 = Kozur, 1978, pl. 4, fig. 11 = Bando et al., 1980, pl. 4, fig. 10), and in one specimen of *N. svalbardensis* Szaniawski and Malkowski. Henderson and McGugan (1986) included lateral bladed specimens in this species, though none were found during this study.

At least one of the paratypes of *N. pequopensis* (Behnken 1975a, pl. 1, figs. 19,20) has a platform that is broader posterior of the midpoint, and platform nodes that flare outward. This specimen (and one other that is similar) occurred at a higher stratigraphic level than the holotype and were regarded by Behnken (1975a) as "advanced forms". However, they may be representative of the *N. ruzhencevi* group (see below).

Neostreptognathodus ruzhencevi Kozur 1976

Plate 2, figs. 9,11

?p. 1975 *Neostreptognathodus pequopensis* Behnken (a), p. 310, pl. 1, figs.?19,20.
1976 *Neostreptognathodus ruzhencevi* n. sp. — Kozur and Mostler, p. 15-16, pl. 2, figs. 1-3.
? 1979 *Neostreptognathodus* sp. A — Szaniawski and Malkowski, p. 252, pl. 8/2,6.
? 1986 *Neostreptognathodus pnevi* Kozur and Movshovich — Henderson and McGugan, p. 232, fig. 8/11-14.

Diagnosis:
A species of *Neostreptognathodus* in which anterior parapets merge with the blade. The platform bears about 8 transverse ridges and a medial sulcus.

Remarks:
There is some doubt about the true identity of this species. The original description of this species corresponds closely to the morphology exhibited by juvenile neostreptognathodids associated with *N.* aff. *N. ruzhencevi* (q.v.) and *N. sulcoplicatus*. Similarly, the synonymy includes only small specimens, as does the count presented in Table 2. However, Kozur and Mostler (1976, p. 15) stated that this is a very large form. Other authors have interpreted the species differently.

Neostreptognathodus ruzhencevi Kozur 1976
alpha morphotype

Plate 2, fig. 16

1983 *Neostreptognathodus ruzhencevi* Kozur — Wardlaw (*in* Mytton et al.), p. 299, 302, fig. 12: 15-19.

1986 *Neostreptognathodus ruzhencevi* Kozur and Movshovich (sic) -Henderson and McGugan, p. 232, fig. 8/ 8 (?6,7).

Diagnosis:
An asymmetric morphotype of the *ruzhencevi* group with one anterior platform parapet joined to the blade and the other separated from it by a continuation of the medial furrow. The joined parapet generally has subdued nodes or is smooth.

Remarks:
This morphotype corresponds to *N. ruzhencevi* Kozur 1976 sensu Wardlaw (in Mytton et al. 1983), and Henderson and McGugan (1986). It is clearly not the same species originally described by Kozur and Mostler (1976). Wardlaw (op. cit.) stressed a lateral position for the blade at the platform junction, and smooth or almost smooth anterior parapets in *N. ruzhencevi*. Neither of these features were specifically mentioned by Kozur and Mostler (1976), nor are they evident in the illustrations of the type material. Henderson and McGugan (1986, p.232) also interpreted *N. ruzhencevi* as lateral-bladed and stressed the flexture of the blade at the platform junction.

Recently, Behnken et al. (1986) have interpreted *N. ruzhencevi* as including forms that do not have a joined lateral blade. These differ from *N.* aff. *N. ruzhencevi* in having subdued nodes on the parapets.

Neostreptognathodus aff. *N. ruzhencevi* Kozur 1976

Plate 2, figs. 9-11,19,21,?24

Diagnosis:
A species of *Neostreptognathodus* characterized, in later growth stages, by an asymmetric anterior platform and a subcentral blade. The platform bears strong transverse ridges and a medial sulcus.

Description:
The blade is approximately the same length as the platform. In profile, the highest point of the blade lies near its anterior end, in front of which there may be one or two small denticles. In total there are 8-10 blade denticles which generally diminish in size posteriorly. The posterior 1/4 of the blade often consists of completely fused denticles forming a smooth topped ridge. In rare forms, the posterior blade may be thickened by lateral outgrowths. In upper view, the platform is usually lachrymiform or vase shaped with the widest point occurring a little posterior of midlength; the anterior usually narrows markedly to form two subparallel parapets.

In associated early growth stages (*see N. ruzhencevi*), the blade/platform transition appears 'smooth' in the sense that the first pair of denticles are small and unflared. At this stage, the parapet denticles do not appear to be clearly separated from the blade (Plate 2, fig. 11). In larger specimens, the blade and at least one parapet are separated, and the blade joins the platform submedially. The anterior-most denticle on the parapet farthest from the blade is often enlarged and may be slightly flared outward; on this same side the posterior platform nodes tend to be more laterally elongate compared with the opposing nodes where the platform margin tends to be straighter. This imparts an asymmetry to the platform.

Platform sculpture in juveniles (*see N. ruzhencevi*) consists of two rows of equidimensional nodes that are directed obliquely outward. The nodes become ridge-like with growth, and mature specimens usually have 10-12, less commonly up to 15 pairs of transverse ridges, which are more distantly spaced posteriorly. Toward the medial furrow, the ridges tend to be oriented obliquely anteriorward, particularly in the posterior 2/3 of the platform. If sufficiently well preserved (Plate 2, fig. 12 shows the effects of recrystallization), the ridges bear a line of pustules on their crest; in some gerontic specimens the pustules may become irregularly developed, particularly near the posterior end. At all growth stages, the two platform margins are separated by a distinct furrow that is slightly to markedly broader posteriorly.

The posterior end of the platform is commonly pointed in which case the hindmost pair of nodes are joined. In gerontic specimens, rounded posteriors may occur and the ridges become oriented radially around the platform margin. The basal cavity is broadly flared laterally and, when preserved intact, extends beyond the posterior platform.

Remarks:
A distinction between lateral and medial blades has previously been emphasized for taxonomic differentiation in *Neostreptognathodus*. However, in the present collections, a complete gradation exists between lateral and medially bladed morphotypes. At one extreme, there are rare specimens with true lateral blades (identified above as *alpha* morphotype, q.v.), whereas at the other end of the spectrum there are specimens with medial blades, which are probably indistinguishable from *N. sulcoplicatus* (q.v.). The majority of *Neostreptognathodus* specimens from Kamloops appear transitional between the two. Phylogenetic trends in *Neostreptognathodus* populations probably involved changes in the ratio of these symmetry variations, and although separa-

tion of these morphotypes is probably artificial, it is done in order to maximize their stratigraphic utility.

Comparisons:
Discrimination of *Neostreptognathodus* species presents many problems arising from both ontogenetic variation and intraspecific symmetry variation as documented here. An added problem arises from poor illustration and variable interpretation of type material. The following review focuses on some of the problems.

In common with *N. ruzhencevi*, the present species shows variable posterior outlines from acute to rounded, the platform is widest near the middle, the posterior portion of the blade is often fused, and lateral widening of the blade's posterior denticles sometimes occurs. However, *N. ruzhencevi* Kozur 1976 "almost always" has 8 pairs of nodes in contrast with the 10-15 seen in the Kamloops neostreptognathodids. Also, in *N. ruzhencevi*, the platform "passes smoothly" into the blade (Kozur and Mostler, 1976, p.16), that is the parapets do not flare out at the anterior end of the platform. This anterior configuration is typical of small specimens associated with *N.* aff. *N. ruzhencevi*, but larger specimens have an abrupt blade/ platform junction.

N. newelli Wardlaw and Collinson 1984 commonly has more (12-17) pairs of platform nodes than *N.* aff. *N. ruzhencevi*. Also, the former species has a narrower median groove, more joined posterior ridges, and anterior parapets that tend to be smooth. According to Wardlaw and Collinson (1984, p. 270), *N. newelli* is an asymmetrical species, although the original illustrations of this species include a wide range of variation in blade position.

N. exsculptus Igo 1981 is close to *N. newelli*, but the former does not have fused anterior parapets (Igo and Hisada, 1986, p. 523). Atypically, *N. exsculptus* sensu Henderson and McGugan (1986) has a markedly lateral blade, and some tranverse ridges that extend across the medial furrow.

N. aff. *N. ruzhencevi* differs from *N. pequopensis* Behnken in early growth stages by having nodes that flare outward rather than upward, and in later growth stage by having laterally enlarged nodes. Although most of the specimens included in *N. svalbardensis* Szaniawski and Malkowski 1979 have obliquely oriented platform nodes, Bando et al. (1980, p.8) regarded most of these species (but not the holotype: see *N. clarki*) as *N. pequopensis*; node orientation may serve to distinguish the two species. The blade of *"N. svalbardensis"* (Szaniawski and Malkowski 1979, pl.6, fig.5) is shorter than that of the *N. ruzhencevi* group.

N. tschuvaschovi Kozur 1976 has a characteristic lachrymiform shape with the widest part at or near the posterior end of the platform, and distinctive radial ribs posteriorly. In *N.* aff. *N. ruzhencevi*, the posterior platform generally terminates acutely and is only rounded with radial ribs in gerontic specimens in which the number of platform ridges is significantly more than the 8 pairs common in *N. tschuvaschovi*. Contrary to the original description of *N. tschuvaschovi*, Wardlaw (*in* Mytton et al., 1983) has interpreted the species to include forms with pointed posterior margins, subparallel platform margins, and lateral blades.

N. pnevi Kozur and Movshovich 1979 (*see* Movshovich et al., 1979) differs from *N.* aff. *N. ruzhencevi* in having reduced anterior parapet nodes. This is not the case in *N. pnevi* of Henderson and McGugan (1986); these authors stressed the "smooth" (lack of pustules) nodes of their *N. pnevi* (possibly due to recrystallization?).

Neostreptognathodus sulcoplicatus
(Youngquist, Hawley and Miller 1951)

Plate 2, figs. 12-15,17,18,20,22

1951 *Streptognathodus sulcoplicatus* n. sp. — Youngquist, Hawley and Miller, p. 363, pl. 54, figs. 7-9,16,17,22-24.
? 1975 *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley and Miller) — Behnken (a), p. 311-12, pl. 1, fig. 3(only).
? 1982 *Neostreptognathodus* sp. B — Wardlaw et al., fig. 1B.
? 1986 *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley and Miller) — Wardlaw and Collinson, fig.18/ 5?,6-16.
1986 *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley and Miller) — Behnken et al., p. 184-5, fig. 4/ 9 (with synonymy through 1983).

Diagnosis:
A symmetrical species of *Neostreptognathodus* in which the anterior parapets are clearly separated from, and variably flare outward on both sides of, a central blade. Both platform margins bear nodes or ridges separated by a median sulcus that broadens posteriorly.

Remarks:
All of the Kamloops neostreptognathodids that have a symmetrical anterior platform, a medial blade and transverse platform ridges are combined here, regardless of the degree of outflaring of the anterior parapets. In very few specimens is the latter feature strongly displayed (e.g. Plate 2, fig. 14).

As discussed under *N.* aff. *N. ruzhencevi*, these symmetrical specimens constitute end members of a series that includes asymmetrical neostreptognathodids. All the specimens of this series have similar platform ornamentation. The Kamloops population that includes these elements referred to *N. sulcoplicatus* differs from topotype populations because the latter contain only forms with outflaring parapets (C. Henderson, pers. comm., 1987). This suggests that the Kamloops material is perhaps older, but we recognize no objective way of separating single specimens.

One specimen referred to *N. sulcoplicatus* by Behnken (1975a, pl. 1, fig. 3) exhibits a slight asymmetry to the anterior platform with only one margin flaring outward; it also has relatively few ridges on the platform. Similarly, at least one specimen included in this species by Wardlaw and Collinson (1986, fig. 18/5) has a blade near one margin and

smooth anterior parapets. These are not features generally attributed to *N. sulcoplicatus*, which further emphasizes the difficulty in speciating the genus.

Specimens illustrated by Clark and Ethington (1962, pl. 2, fig. 3) are narrower than *N. sulcoplicatus* and may be *N. newelli*. A specimen that fits our concept of *N. sulcoplicatus* was called *N.* sp. B by Wardlaw et al. (1982), although this specimen was only figured and not described.

Behnken et al. (1986, p. 184) illustrated ramiform elements of this species, but only the platform elements were considered for our synonymy.

Sweetognathus behnkeni Kozur 1975

Plate 1, fig. 21

1975 *Sweetognathus behnkeni* n. sp. — Kozur, p. 3-4.
1986 *Sweetognathus behnkeni* Kozur — Ritter, p. 149-50, pl. 2, figs. 11-15 (with synonymy through 1983)
1987 *Sweetognathus behnkeni* Kozur — Suarez Riglos et al., pl. 19.3, figs. 17-23,?24.
p. 1987 *Sweetognathus whitei* (Rhodes) — Suarez Riglos et al., pl. 19.3, figs. 13,16 (only).
1987 *Sweetognathus behnkeni* Kozur — Ritter, pl. 23.1, figs. 10,12.

Diagnosis:
A large species of *Sweetognathus* with a broad biconvex platform bearing obliquely oriented ridges in the posterior part.

Remarks:
A single specimen occurs with smaller sweetognathids referred to *S. whitei*. The platform has its maximum width at its middle rather than farther anterior. Also, the ribs are less obliquely oriented compared to typical *S. behnkeni*; these differences are presently regarded as intraspecific. As documented by Ritter (1986), *S. behnkeni* is most commonly recognized in later growth stages.

Sweetognathus inornatus Ritter 1986

Plate 1, fig. 6

1984 *Sweetognathus aff. S. whitei* (Rhodes 1963) — Orchard (b), p. 213, pl. 23.1, fig. 1,2.
1986 *Sweetognathus inornatus* n. sp. — Ritter, p. 150, pl. 3, figs. 1,6,12-15; pl. 4, figs. 2,9,13,14 (with synonymy through 1981).
1987 *Sweetognathus* n. sp. A — Ritter, pl. 23.1, figs. 1,2.
p. 1987 *Sweetognathus whitei* (Rhodes) — Suarez Riglos et al., pl. 19.2, figs. 10-12 (only).
1987 *Sweetognathus* sp. aff. *S. whitei* (Rhodes) — van den Boogaard, p. 29, fig. 6E,9A.

Diagnosis:
A long-bladed species of *Sweetognathus* with a simple carina consisting of transversely ovoid, pustulose nodes. A longitudinal ridge is generally absent.

Remarks:
As discussed by Orchard (1984b), separation of the present species from early growth stages of *Sweetognathus whitei* is difficult because of recapitulation. Broad noded forms appear early during ontogeny in the younger species, *S. whitei*, whereas in the present species, the nodes never become very broad. In *S. inornatus* the medial ridge is either absent or subtle.

Several other "simple" sweetognathids (Group II of Ritter, 1986) resemble *S. inornatus* at some or all stages of growth. The Wolfcampian *S. merrilli* Kozur 1975, from the Council Grove Group of Kansas, has a similar platform configuration to *S. inornatus* in early growth stages (e.g. Kozur, 1978, pl.3, fig.2), but a relatively short blade with a conspicuous high anterior denticle.

The upper Artinskian (Baigendzhinian) species *S. bogoslovskajae* Kozur 1976 may also be distinguished by its anteriorly very high and deflected free blade. *S. bogoslovskajae* also has more upstanding discrete nodes than both *S. inornatus* (Ritter, 1986, p. 150) and *S. merrilli* (Kozur and Mostler, 1976, p.19). See also *'S.' adjunctus* (Behnken, 1975a).

Sweetognathus whitei Rhodes 1963

Plate 1, figs. 10,11,13,14,16,20

1963 Spathognathodus whitei n. sp. — Rhodes, p. 404-5, pl. 47, figs. 4,9,10,25 (not fig. 26 = S. inornatus, after Ritter).
1984 *Sweetognathus whitei* Rhodes — Orchard (b), p. 213, pl. 23.1, figs. 3-5,8 (with synonymy through 1981).
1986 *Sweetognathus whitei* Rhodes — Ritter, p. 151-2, pl. 3, figs. 2,4,8-11,16-21 (with additional synonymy).
1986 *Sweetognathus whitei* Rhodes — Henderson and McGugan, p. 233, fig. 7/4-7.
1986 *Sweetognathus whitei* Rhodes — Igo and Hisada, p. 523, pl. 97, figs. 16-19.
p. 1987 *Sweetognathus whitei* Rhodes — Suarez Riglos et al., pl. 19.2, figs. 9,13 (only); pl. 19.3, figs. 12,14,15,?25 (only).
1987 *Sweetognathus whitei* Rhodes — Ritter, pl. 23.1, figs. 3?,11.

Diagnosis:
A long bladed, generally symmetrical *Sweetognathus* with a narrow platform on which clearly differentiated pairs of nodes are transversely connected by ridges that are longitudinally linked by a narrow medial ridge. Transverse ridges are broadest about platform midlength.

Remarks:
The original diagnosis for *S. whitei* described the low median ridge lying below the denticles, so it is not conspicuous from the side. However, several specimens from Kamloops (e.g. Plate 1, fig. 14), have a medial ridge clearly lying above the level of the platform denticles. Similarly, contrary to the original description, some specimens have

posterior nodes that are closely spaced and not separated by an interval about equal to their anterior — posterior length. These forms are nevertheless included in *S. whitei*. Other specimens included with question in the synonymy lists (Suarez Riglos et al., 1987; Ritter, 1987) have only a partially developed longitudinal ridge; Kozur and Mostler (1976, p. 19) differentiated similar forms as *S.* n. sp. aff. *whitei*.

As in *Neostreptognathodus* aff. *N. ruzhencevi*, *S. whitei* from Kamloops shows symmetry variation: rare specimens have a blade that joins the platform slightly off-centre, node pairs of unequal size on the platform, and/ or posterior blade denticles laterally enlarged on one side only (Plate 1, fig. 13). Further asymmetry is displayed by one specimen (Plate 1, figs. 15,20) in which the posterior medial ridge is displaced laterally, and the lateral nodes are more differentiated (*see Neostreptognathodus pequopensis*).

The anteriorly asymmetric specimens resemble *Sweetognathus subsymmetricus* Wang et al., 1987 from the Kufeng Formation of Longtang, China, a Guadalupian correlative according to Wang et al. (1987). However, the Chinese species is characterized by a more lateral blade position than any specimen from Kamloops.

Several additional broad-noded *Sweetognathus* species (Group III of Ritter, 1986) occur in the Permian, although, as in *S. whitei*, the intraspecific variability of each has yet to be defined. Both *S. guizhouensis* Bando et al., 1980 (from the Chihsia Stage) and *S. paraguizhouensis* Wang et al., 1987 (from the Makou Stage) of South China differ from the present species in that the anterior-most rib is as long as the following ones. In *S. whitei*, rib length increases progressively to the platform midlength.

S. hanzhongensis (Wang, 1978), from the 'mid' Permian Makou Formation of China, is regarded as the forerunner of *S. iranicus* (Bando et al., 1980, p.5). Carina nodes are less expanded transversely and closer together longitudinally than in *S. whitei*, and the anterior platform appears flattened.

The youngest *Sweetognathus* species, *S. iranicus* Kozur, Mostler, and Rahimi-Yazd 1975, from the Abadehan of central Iran, differs from *S. whitei* in profile. The former has a distinctly arched platform with nodes that become higher posteriorly up to the platform midlength, and a high, relatively short blade with fused posterior denticles. *S. sweeti* Kozur, Mostler, and Rahami-Yazd, 1975, also from the Abedehan, differs in having a wedge-shaped medial furrow near the platform/free blade junction.

'Sweetognathus' ? *adjunctus* Behnken 1975

Plate 1, figs. 7-9,19

? 1975 *Sweetognathus adjunctus* n. sp. — Behnken (a), p. 309, pl. 1, figs. 5-8.

Description:
A small sweetognathid with 6-7 slightly expanded, oval, pustulose carina nodes, a narrow lachrymiform basal cavity extending far anteriorly, and a short blade bearing 3-4 laterally compressed denticles, the second of which is the largest.

Remarks:
A single, small specimen recovered from a stratigraphic level higher than *Sweetognathus whitei* is tentatively referred to *'S.' adjunctus* (Behnken, 1975a). The latter is a poorly known species characterized by a laterally bowed posterior end and, in later growth stages, by transversely broadened, asymmetric nodes; there is no longitudinal ridge. Since the Kamloops specimen is small, these features are not well developed, hence the question mark.

The short blade of this specimen is distinctive and sets it apart from the older, long bladed group of *S. inornatus* and its derivatives. The Kamloops species (?and other younger sweetognathids) may be unrelated to the former. It may have evolved from *Hindeodus*, or a similar short, high bladed form. For this reason, the genus *'Sweetognathus'* is kept in quotes.

The upper Artinskian (Baigendzhinian) species *S. bogoslovskajae* Kozur 1976 also has a high free blade and simple carina nodes. This species appears to differ in having a blade that is both higher anteriorly and laterally deflected; Kozur and Mostler (1976, p. 19) regarded the two species as morphologically close.

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Plate 1

All views are upper unless stated otherwise. Numbers in brackets refer to sample numbers in Text Figure 1 and Tables 1-3. (1984) indicates specimens re-illustrated from Orchard (1984b).

Figures 1-5. *Adetognathus paralautus* Orchard. 1,2. Lateral and upper views, GSC 68918, x60, GSC loc. no. C-87090g (1984); 3,4. Upper and lateral views of holotype GSC 68923, x70, x80, GSC loc. no. C-87090b (1984); 5. GSC 81070, x80, GSC loc. no. C-116054 (K4). Note incipient platform development on anterior outer margin.

Figure 6. *Sweetognathus inornatus* Ritter. GSC 68899, x100, GSC loc. no. C-87090f (1984).

Figures 7-9,19. *'Sweetognathus' ?adjunctus* (Behnken). Two upper, a lateral and carina detail views, GSC 81071, x80, x110, x110, x100, GSC loc. no. C-116793 (E3). Early growth stage.

Figures 10,11,13-15,20. *Sweetognathus whitei* (Rhodes). 10. GSC 81072, x80, GSC loc. no. C-116799 (K20); 11. GSC 81073, x80, GSC loc. no. C-116069 (K19); 13,14. Upper and lateral views, GSC 81075, x80, GSC loc. no. C-116069 (K19); 15,20. Upper view and detail, GSC 81076, x80, x600, GSC loc. no. C-117799 (A6).

Figures 12,16-18. *Diplognathodus augustus* Igo. 12,18. Upper and oblique-lateral views, GSC 81075, x80, x90, GSC loc. no. C-116059 (K9); 16,17. Upper and oblique-lateral views, GSC 81077, x80, x90, GSC loc. no. C-118800 (L4).

Figure 21. *Sweetognathus behnkeni* Kozur. GSC 81078, x80, GSC loc. no. C-116071 (W2).

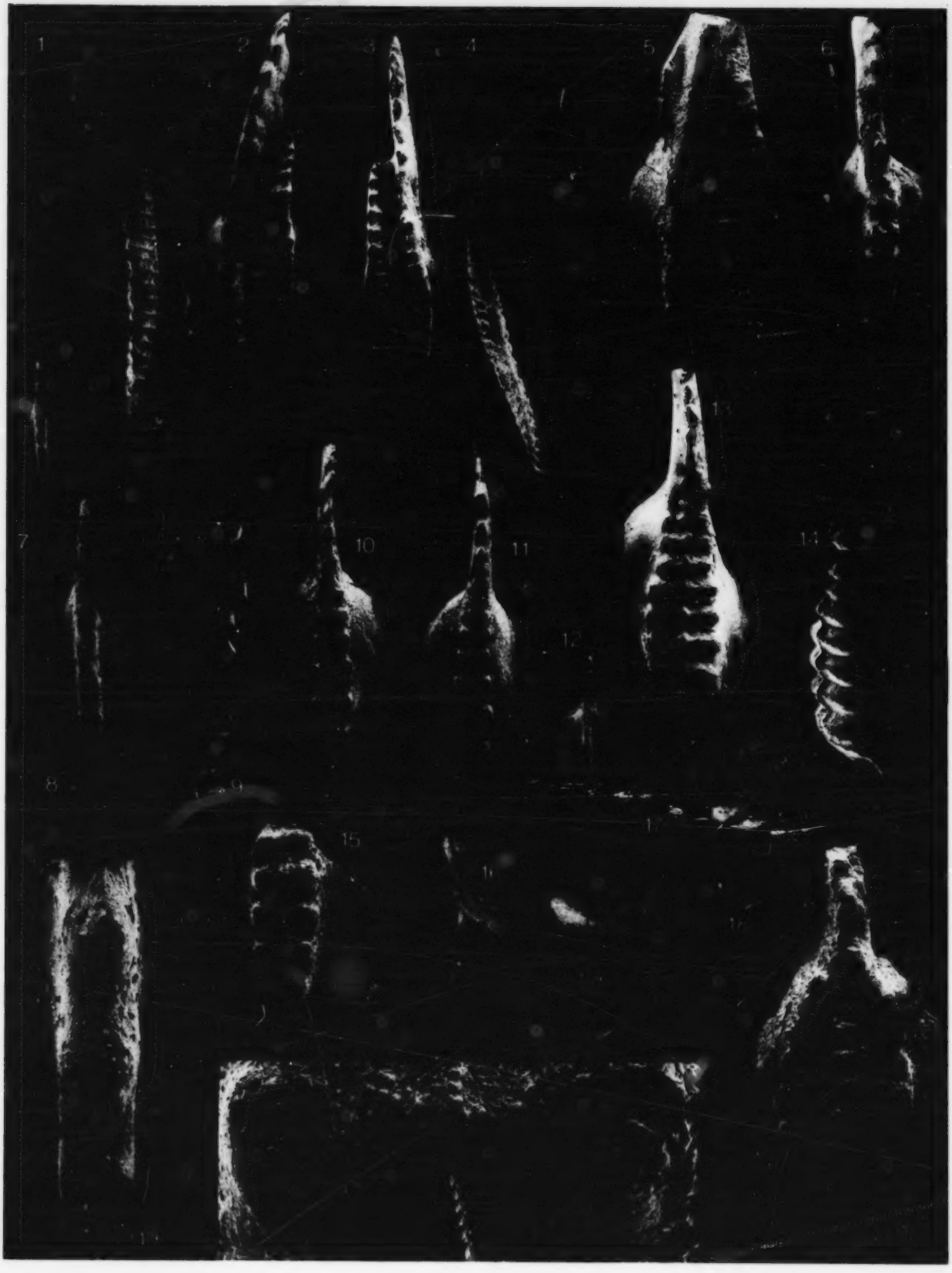

Plate 2

All views are upper unless stated otherwise. Numbers in brackets refer to sample numbers in Text Figure 1 and Tables 1-3.

Figures 1-6. *Neostreptognathodus pequopensis* Behnken. 1. GSC 81079, x160, GSC loc. no. C-116792 (E2). Note unequal development and longitudinal rib; 2,3. GSC 81080, x80, x110, GSC loc. no. C-118855 (T5); 4. GSC 81081, x80, GSC loc. no. C-118855 (T5); 5. GSC 81082, x80, GSC loc. no. C-116766 (I1); 6. GSC 81083, x80, GSC loc. no. C-116792 (E2).

Figure 7?,8. *Neostreptognathodus clarki* Kozur. 7?. GSC 81084, x80, GSC loc. no. C-117799 (A6); 8. GSC 81069, x80, GSC loc. no. C-118862 (T11).

Figures 9-24. *Neostreptognathodus ruzhencevi* Kozur — *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley and Miller) group.

Figures 9,11. *Neostreptognathodus ruzhencevi* Kozur. GSC 81085, x80, x180, GSC loc. no. C-118800 (L4). Early growth stage. Compare platform shape and node orientation with Figure 2.

Figures 10,19,21,?25. *Neostreptognathodus* aff. *N. ruzhencevi* Kozur. 10. GSC 81086, x80, GSC loc. no. C-118804 (L5); 19. Anterior platform fragment, GSC 81093, x80, GSC loc. no. C-116765 (H3); 21. GSC 81095, x70, GSC loc. no. C-116794 (E4). Mature specimen with rounded posterior; ?25. GSC 81097, x80, GSC loc. no. C-116794 (E4). Posterior fragment of gerontic specimen with *'tschuvaschovi'* morphology of radial ribs.

Figure 16. *Neostreptognathodus ruzhencevi* Kozur, alpha morphotype. nov. Anterior platform fragment, GSC 81091, x80, GSC loc. no. C-118811 (T1).

Figures 12-15,17,18,20,22. *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley and Miller). 12. GSC 81087, x80, GSC loc. no. C-116772 (F3). Juvenile specimen; 13. GSC 81088, x80, GSC loc. no. C-118800 (L4); 14. GSC 81089, x80, GSC loc. no. C-118800 (L4); 15. GSC 81090, x80, GSC loc. no. C-118800 (L4). Specimen with marked outflaring of parapets; 17,18. Upper and lateral views, GSC 81092, x70, GSC loc. no. C-116794 (E4); 20. GSC 81094, x70, GSC loc. no. C-118800 (L4); 22. GSC 81096, x80, GSC loc. no. C-116794 (E4).

Figures 23, 24. *Neogondolella gujioensis* Igo. GSC 81112, x60, GSC loc. no. C-116781 (F12). Oblique and upper views; high anterior blade is broken.

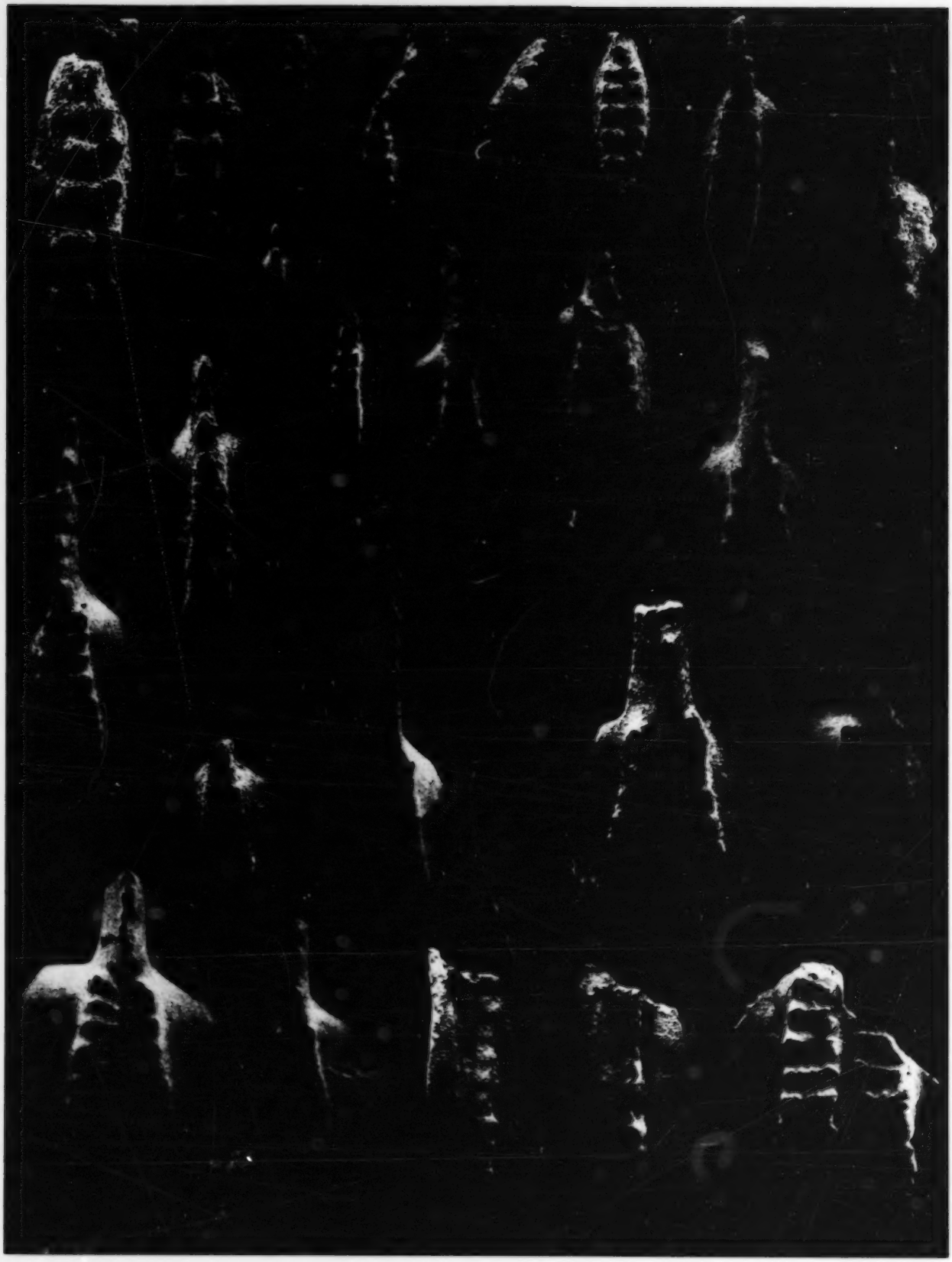

Plate 3

All views are upper unless stated otherwise. Numbers in brackets refer to sample numbers in Text Figure 1 and Tables 1-3.

Figures 1-3,7-9,?14. *Neogondolella bisselli* (Clark and Behnken). 1. GSC 81098, x80, GSC loc. no. C-116792 (E2); 2. GSC 81099, x60, GSC loc. no. C-116764 (H2); 3. Lower view, GSC 68909, x100, GSC loc. no. C-87090b (1984); 7-9. Lateral, upper and lower views of advanced form, GSC 81102, x60, GSC loc. no. C-116794 (E4);?14. GSC 81106, x80, GSC loc. no. C-118799 (L3).

Figures 4-6. *Neogondolella* n. sp. A. 4,5. Upper and lower views, GSC 81100, x70, GSC loc. no. C-117800 (F1); 6. GSC 81101, x80, GSC loc. no. C-116765 (H3).

Figures 10,11,?12,15,16,21. *Neogondolella intermedia* Igo. 10,11. Lower and upper views, GSC 81103, x70, GSC loc. no. C-118807 (L7b);?12. Posterior fragment, GSC 81104, x80, GSC loc. no. C-116793 (E3); 15,16. Lateral and upper views, GSC 81107, x90, x80, GSC loc. no. C-116793 (E3); 21. GSC 81110, x70, GSC loc. no. C-116780 (F11).

Figures 13?,17,22-24. *Neogondolella idahoensis* (Youngquist, Hawley and Miller).?13. Posterior fragment of late growth stage, GSC 81005, x80, C-118408 (W3); 17. Posterior fragment, GSC 81008, x80, GSC loc. no. C-118408 (W3); 22-24. Lower, oblique lateral and upper views, GSC 81111, x50, Gsc loc. no. C-116756 (G1a).

Figures 18-20. *Neogondolella idahoensis* n. subsp. A. 18-20. Oblique lateral, upper and lower views, GSC 81109, x50, x60, x60, GSC loc. no. C-116793 (E3).